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# Dinâmica de diversificação de Placentalia (Mammalia): integrando o registro fóssil com filogenias moleculares

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# Diversification dynamics of Placentalia (Mammalia): integrating the fossil record with molecular phylogenies

Dissertação apresentada ao
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Orientador: Prof$^{\text{o}}$ Dr. Tiago Bosisio Quental

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**Dinâmica de diversificação de Placentalia (Mammalia): integrando o registro fóssil com filogenias moleculares**

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## Comissão Julgadora:

Prof(a). Dr(a).

Prof(a). Dr(a).

Prof. Dr. Tiago Bosisio Quental
Orientador

Aos meus avós, Junio e Daisy,
pelo carinho e suporte
nesses 8 anos de faculdade

“[...] You can experience the wonder of seeing them for the first time,
the thrill of discovery, the incredible, visceral feeling of doing something no
one has ever done before, seen things no one has seen before,
know something no one else has ever known.

No crystal balls, no tarot cards, no horoscopes.
Just you, your brain, and your ability to think.

Welcome to science. You’re gonna like it here.”

- Phil Plait

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# 1 Introduction

The subclass Placentalia (class Mammalia) has a huge diversity of morphologies, ecologies, physiologies, and life histories. This lineage encompasses the 21 extant orders of Eutheria, including more than 5,000 species (Wilson and Reeder, 2011). The placentals are amongst the most studied vertebrates groups, yet some aspects of their evolution have not been fully understood (e.g., Archibald and Deutschman, 2001; Springer et al., 2003).

Like most of organisms, the placental mammals have great variation in the number of species among its genera, families, and orders (Yu et al., 2012). The imbalance in the number of species reflects the complex interactions among speciation, extinction, and dispersion that generated the extant diversity of Placentalia (Jones and Safi, 2011). Each subgroup experienced different diversification dynamics (Davies et al., 2008), with many groups now fully extinct (Kemp, 2005) or experiencing a decline in its diversity (Quental and Marshall, 2013). Indeed, it is possible to infer several independent changes in the diversification rates (i.e., speciation rate - extinction rate) for the different orders and families of placental mammals (Venditti et al., 2011; Yu et al., 2012). This pattern cannot be explained only by abiotic factors or biotic interactions, which suggests that the evolution of different traits might have played an important role in the changes in the diversification rates (Davies et al., 2008).

Many studies have explored the positive effects of traits on the diversification of a lineage, especially in cases of adaptive radiation (e.g., Gavrilets and Losos, 2009; Wagner et al., 2012; Shah et al., 2012). On the other hand, the possible negative effects of traits on the diversification dynamics have been for the most part overlooked (but see Van Valkenburgh, 1999; Van Valkenburgh et al., 2004). This lack of studies might be due to problems in finding a candidate trait, given that it is difficult to see how a lineage with a trait that has a negative effect on its diversification was able to diversify in the first place (Rankin and López-Sepulcre, 2005). Such diversification pattern would probably require a complex evolutionary dynamics in which the given trait could confer some selective advantages in some taxonomic or time scales, but would be selected against in other scales. A first approach to find a candidate trait would be to investigate how lineages with diversity decline are distributed in the phylogeny. In case the decline in diversity is more common in a given part of the phylogeny (i.e., show a significant phylogenetic signal; Nunn, 2011), it would indicate that these lineages share an evolutionary history that makes them more prone to the decline. Although the effect of a trait on the diversification is not conditioned on this phylogenetic aggregation (Tomiya, 2013), such pattern would foster the search for traits that show the same phylogenetic distribution.

Several traits may be related to the waning and waxing of the diversity, like geographic range, trophic level, dietary and habitat specialization, body size, generation time, and population density (Purvis et al., 2000). Each of these traits can affect the diversification of a lineage, however, body size is directly or indirectly linked to many, if not most, life history characters of an organism (Blueweiss et al., 1978; Roy, 2008), hence it is widely used as proxy for ecology in evolutionary studies. Given its importance, the causes of body size evolution have been thoroughly studied in several lineages (e.g., Hutchinson and MacArthur, 1959; Kozlowski and Gawelczyk, 2002; Clauset and Erwin, 2008; McClain and Boyer, 2009; Payne et al., 2009; Heim et al., 2015), and in particular their relation to physiological, ecological, and evolutionary factors (Smith and Lyons, 2013). In mammals this is especially true (e.g., Gardezi and da Silva, 1999; Smith et al., 2004; Liow et al., 2008; Smith and Lyons, 2011; FitzJohn, 2012; Tomiya, 2013; Slater, 2013; Saarinen et al., 2014). Particular interest has been devoted to understand the tendency of body size to increase with time, known as Cope's rule, as well as to explain the distribution of body size of extant species. Nevertheless, the dynamics of body size evolution of many placentals lineages is not fully understood.

The distribution of body size in Placentalia is highly asymmetric with a high frequency of small species and a long right tail (Figure 1.1). Collectively, previous studies suggest that the evolution of body size is the result of several selective pressures acting in different time scales and hierarchical levels, but disagree on the importance of various potential key factors that might influence the evolution of body size (Gardezi and da Silva, 1999; Hone and Benton, 2005; Allen et al., 2006; McNab, 2010). For instance, Clauset and Erwin (2008) argue that physiological constraints might impose a minimum viable body size (for mammals around 2g), while Brown et al. (1993) suggests that the high frequency of small species is attributed to a physiologically optimum size (for mammals around 100g). Others suggest that the small frequency of mammals with large body size (the long right tail on Figure 1.1) have been generated by higher extinction risk and/or lower speciation probability of larger mammals (Roy, 2008), counterbalanced by short-term competitive advantages related to the increase in size (Brown and Maurer, 1986). Therefore, the body size appears as good candidate to be correlated with the decline in diversity. Natural selection could favor larger individuals (Trivers, 1972; Blueweiss et al., 1978; Brown and Maurer, 1986; Festa-Bianchet et al., 1998) and that process could eventually lead to a trend towards larger body size at longer time scales (i.e., Cope's rule). However, if this selective advantage was constant we should have a world full of giants, and hence the tendency to increase in size must be counterbalanced at some level (Roy, 2008). Based on that, we expect that lineages composed by larger placentals would be more prone to decline of diversity than lineages composed by smaller placentals.

Another trait that might be associated with the diversity decline of the lineages of Placentalia is the morphological disparity (Foote, 1997), which is related to the occupancy of the niche space (Erwin, 2007). Given that patterns of diversification should be reflected in the niche dynamics (Benton and Emerson, 2007), one would expect that clades with different

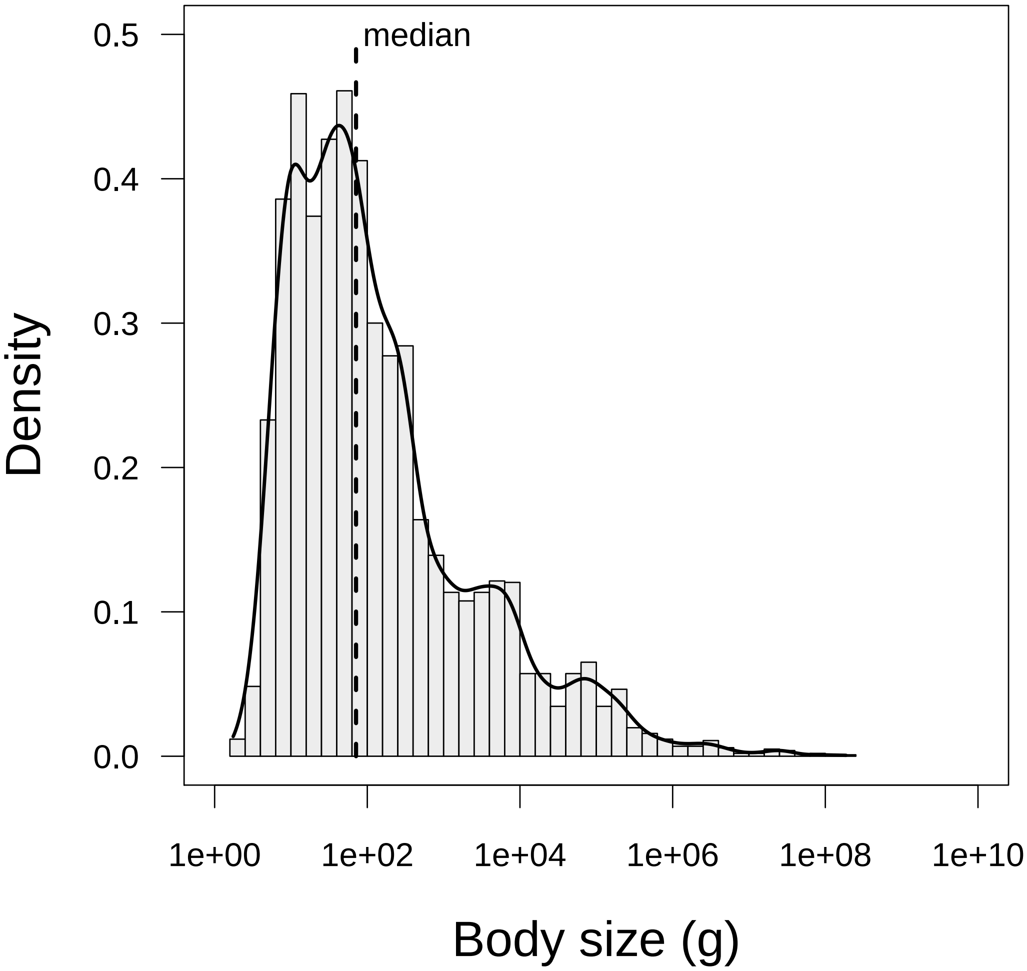


**Figure 1.1:** Distribution of body size for 5,066 species of extant placental mammals. The solid line is the adjusted density curve. The vertical line indicates the median of 71.23g. The x-axis is in $log_{10}$ scale otherwise the distribution right tail would look extremely long. The body size estimates are based on the "EltonTraits database" (Wilman et al., 2014).

levels of morphological constraint might have different diversification dynamics and species richness (e.g., McClain and Boyer, 2009; Goswami et al., 2014, and references therein). Thus, we also expect the morphological disparity to be correlated with the decline in diversity.

Additionally, recent studies (e.g., Cardillo et al., 2005; Butchart et al., 2010) indicate that some traits are associated with the extinction risk of extant mammals. However, it is not clear whether the traits correlated with extinction nowadays are the same ones that are related to the decline in diversity in the past. This comparison is extremely difficult given that paleontological and neontological studies usually differ in their unity of analysis and temporal scale considered (Purvis et al., 2000). Nevertheless, the patterns of extinction are more easily assessed and here we investigate whether the orders in decline of diversity, inferred from the fossil record, are the ones with higher extinction risk nowadays.

Two general approaches have been used to study diversity dynamics (Harnik et al., 2014): analytical paleobiology and comparative phylogenetic analyzes. Analytical paleobiology is the most direct way of investigating the evolutionary dynamic of a lineage. The analysis of the fossil record enables the direct study of how the diversity changed through time, as well as the direct estimation of the extinction and origination rates, and how these rates varied through time (e.g., Alroy, 2008; Foote, 2000; Raia et al., 2013). Using analytical paleobiology it is also possible to study the relationship between morphological evolution and the rate of diversification (Purvis et al., 2000). However, the fossilization process is imperfect. Only specific traits of certain organisms are preserved and it has been estimated that only 8-10% of the biota may be represented in the fossil record (Forey et al., 2004). This bias makes the direct analysis of the diversification dynamics unfeasible for the majority of the biodiversity (Foote and Miller, 2007; Etienne et al., 2011; Ezard et al., 2011b). Additionally, studies based solely on the fossil record usually lack a phylogenetic framework, and therefore cannot easily incorporate the effect of shared history in their diversification analysis. On the other hand, comparative phylogenetic analysis allows one to study the evolutionary dynamic through molecular phylogenies (Nee, 2006) and, given the great amount of phylogenies available nowadays (e.g., McMahon et al., 2015), the analysis of diversification patterns has almost no taxonomic constraints. In addition, with molecular phylogenies it is possible to properly investigate the relationships of the lineages in the analysis and, hence, analyze how the history of a given trait might affect the diversification dynamics. The increase in the number of available molecular phylogenies led to the development of several methods to estimate the diversification dynamics (e.g., Morlon et al., 2010; Pigot et al., 2010). However, there are many biases in analyzes based only on molecular phylogenies (Quental and Marshall, 2009, 2011). For instance, it is very difficult to determine the diversity trajectory based on the molecular signal (Liow et al., 2010a; Quental and Marshall, 2010; Moen and Morlon, 2014).

Therefore, integrating both the paleontological and neontological approaches is the best way to assess the patterns and processes underlying organismal evolution (Rabosky, 2009; Goswami, 2012; Fritz et al., 2013). Here we used both the fossil record and molecular data to determine the diversification dynamics of Placentalia and investigate different mechanisms that might control the evolutionary success of its lineages.

# 2 Objectives

In this project we investigated the diversification dynamics of Placentalia, focusing in the lineages in decline of diversity. More specifically, we analyzed traits that might make a lineage more prone to the decline in diversity. In addition, we investigate whether the lineages that show a historical pattern of diversity decline are also the ones in higher risk of extinction nowadays.

## 2.1 Specific Objectives

1. Determine which of the 21 orders of Placentalia are in decline of diversity, using the fossil record;
2. Investigate whether the model of decline of diversity has a phylogenetic signal;
3. Test the hypothesis that the differences in body size are related to the decline in diversity;
4. Test the hypothesis that the morphological disparity is related to the diversity decline;
5. Investigate whether the orders in decline of diversity, inferred from the fossil record, are the ones with higher extinction risk nowadays.

# 3 Materials and Methods

In order to study the diversification dynamics of the placental orders we used both fossil information (section 3.1 and 3.2) and a phylogeny based on molecular data (section 3.3). The fossil record was used to determine the diversification history of the orders while taking into account potential biases in the fossil record (section 3.4). The molecular phylogeny was used to study the phylogenetic signal of the traits (section 3.8) and, when appropriate, test for correlation between the traits and the decline in diversity (section 3.9). Finally, we tested the hypothesis of positive correlation between decline of diversity and body mass (section 3.5), as well as the potential correlations between diversity decline and either morphological disparity (section 3.6) or current extinction risk (section 3.7). The materials and methods used are detailed in the sections below.

## 3.1 Datasets

The fossil record was analyzed based on the "Paleobiology Database" (PBdata; Alroy et al., 2015) and the "New and Old Worlds - Database of fossil mammals" (NOW; Fortelius, 2015). Whereas the PBdata contains mainly North America information, the NOW database contains information mainly about Eurasian and African land mammals. We combined these two databases first correcting for typos, and then checking for species synonyms. After that we created a dataset that contains only the occurrences that are resolved to one geological stage (hereafter "stg1"). Each entry in the dataset (i.e., occurrence) represents one spatial-temporal occurrence (e.g., one specimen at a given place and time) and, given that the mean duration of the stages analyzed is 3.43 Million years (My; Appendix III), each specimen must have occurred in one stage only. Hence, the "stg1" dataset is composed of the best data available.

On the other hand, by discarding all occurrences with a resolution worse than the stage resolution, we lose a considerable amount of data (Appendix II). In order to minimize the data loss, we created another dataset that contains the occurrences resolved to one or two stages (hereafter "stg2"). However, there are basically two problems with this dataset: the duration of the occurrences and possible duplicates. As stated above, each fossil occurrence must be restricted to one geological stage. So each occurrence was randomly assigned to one of its stages. This procedure was repeated 1,000 times and each randomization was analyzed separately in order to incorporate the uncertainty of the fossil record (see section 3.4). The second problem is duplicated entries. The same occurrence may appear in both PBdata and

NOW. This is not a problem for the “stg1” dataset, as none of the methods applied here use information about the number of occurrences of each lineage. However, when we randomly resolve each entry of the “stg2” dataset, we may assign the same duplicated occurrence to different stages. If this is the case we may inflate the estimated diversity and the quality of the fossil record. In order to avoid these biases, we removed all potential duplicated entries before the randomization step. For example, lineage A has 7 entries in the “stg2” dataset: 2 occurrences in the Tortonian, 2 occurrences in the Gelasian or Piacenzian, and 3 occurrences in the Piacenzian or Zanclean. After removing the duplicates we would only have 3 entries for lineage A: 1 occurrence in the Tortonian, 1 occurrence in the Gelasian or Piacenzian, and 1 occurrence in the Piacenzian or Zanclean. In this way, the same occurrence cannot appear in the Gelasian and Piacenzian nor in the Piacenzian and Zanclean at the same time. Thus, we have two datasets that were analyzed separately: the more restrictive “stg1”, and the 1,000 randomizations of the “stg2”.

## 3.2 Taxonomic level

The fossil record is the most direct way to access the diversification dynamics of a lineage. However, only a few lineages have a fossil record that allows the analysis of the diversification at the species level (Raup and Sepkoski, 1982; Valentine and Walker, 1986) and paleontological studies generally use taxonomic groups above the species level as the unit of analysis (e.g., Bambach et al., 2004; Foote, 2007; Alroy, 2008; Jablonski, 2008a; Quental and Marshall, 2010). There are two main problems with data from the fossil record: the delimitation of species and the number of fossils available. There are several ways to define fossil species and some methods tend to be biased (Forey et al., 2004). The lineages are more easily defined and the taxonomic uncertainty diminishes for taxonomic units above the species level (Foote and Miller, 2007), which improves the reliability of the analysis of the diversification. Besides, taxonomic levels are hierarchical, which means that at any given time throughout the evolutionary history of a lineage it is expected that the number of families will exceed the number of orders, and the number of orders will exceed the number of classes. This relationship is also found in the fossil record (Valentine, 1974) and higher taxonomic levels have a more abundant fossil record. Therefore, analyses of the fossil record that use higher taxonomic levels are more robust to incompleteness.

On the other hand, when using a higher taxonomic level one assumes that the diversification pattern at the level analyzed reflects the diversification pattern at the species level (Valentine and Walker, 1986). In general, the higher the taxonomic level, the lower the correlation between the diversification dynamics analyzed and the dynamics at the species level (Valentine, 1974). For example, imagine that a given order suffers an extinction event that eliminates 75% of its species, if only one species of each family survives then this event will not be detected in the family level. Therefore, higher taxonomic levels, such as class and order, should be avoided. The most common taxonomic units are genus and family (e.g., Valentine, 1974; Valentine and Walker, 1986; Lloyd et al., 2012). Furthermore, several authors (Valentine, 1974; Raup and Sepkoski, 1982, 1984; Valentine and Walker, 1986) argue for genus as the best compromise between abundance in the fossil record and the reliability of the analysis. In the current study all analyzes were performed at the genus level. Although the analysis at the species level may be possible for some parts of the fossil record and specific orders, genus is the unit of analysis that can be used to best characterize the diversification dynamics of all the 21 orders of Placentalia.

## 3.3 Phylogenies

Placentalia can be divided in four superorders: 1- Afrotheria, comprehends Proboscidea, Sirenia, Hyracoidea, Macroscelidea, Afrosoricida, and Tubulidentata; 2- Xenarthra, composed of Pilosa and Cingulata; 3- Laurasiatheria, composed of Carnivora, Pholidota, Perissodactyla, Chiroptera, Cetacea, Artiodactyla, Soricomorpha, and Erinaceomorpha; 4- Euarchontoglires, comprehends Primates, Dermoptera, Scandentia, Rodentia, and Lagomorpha (Springer et al., 2004; Archibald, 2011). The latter two are usually grouped under the name Boreotheria. Each of these lineages has originated in different regions of the globe. Boreotheria comes from the Laurasia of the Northern Hemisphere, whereas Afrotheria and Xenarthra originated in Africa and South America, respectively (Nishihara et al., 2009). The relationship among these superorders as well as the 21 orders of Placentalia has already been thoroughly studied (Asher et al., 2009; Lee and Camens, 2009; Springer et al., 2004; Song et al., 2012) and, in spite of some minor differences among the proposed hypotheses, the phylogenetic relationships among the placental lineages are well established. The dating of the phylogeny of placentals, on the other hand, is still controversial. The end of the Cretaceous period (65.5±0.3 Ma) is characterized by a mass extinction event: in an interval of 2.5 million years (some estimates indicate less than a year) approximately 76% of the extant species went extinct (Barnosky et al., 2011), including all non-avian dinosaurs. In 2001, Archibald and Deutschman proposed three models of mammals diversification considering the barrier between the Cretaceous and the Paleogene (K-Pg):

- **Explosive model**: the origination of the last common ancestor and the diversification of the crown group (i.e., the clade composed by the last common ancestor of the extant lineages, including all the extinct lineages) of the orders of Placentalia occurred around the beginning of the Paleogene (Figure 3.1.A).
- **Long-fuse model**: the origination of Placentalia and the diversification of its orders occurred during the Cretaceous. Nevertheless, the diversification within each order occurred only in the Paleogene (Figure 3.1.B).
- **Short-fuse model**: some orders diversified in the Cretaceous, right after the origi-

nation of Placentalia. The rest of the orders diversified only in the Paleogene (Figure 3.1.C).

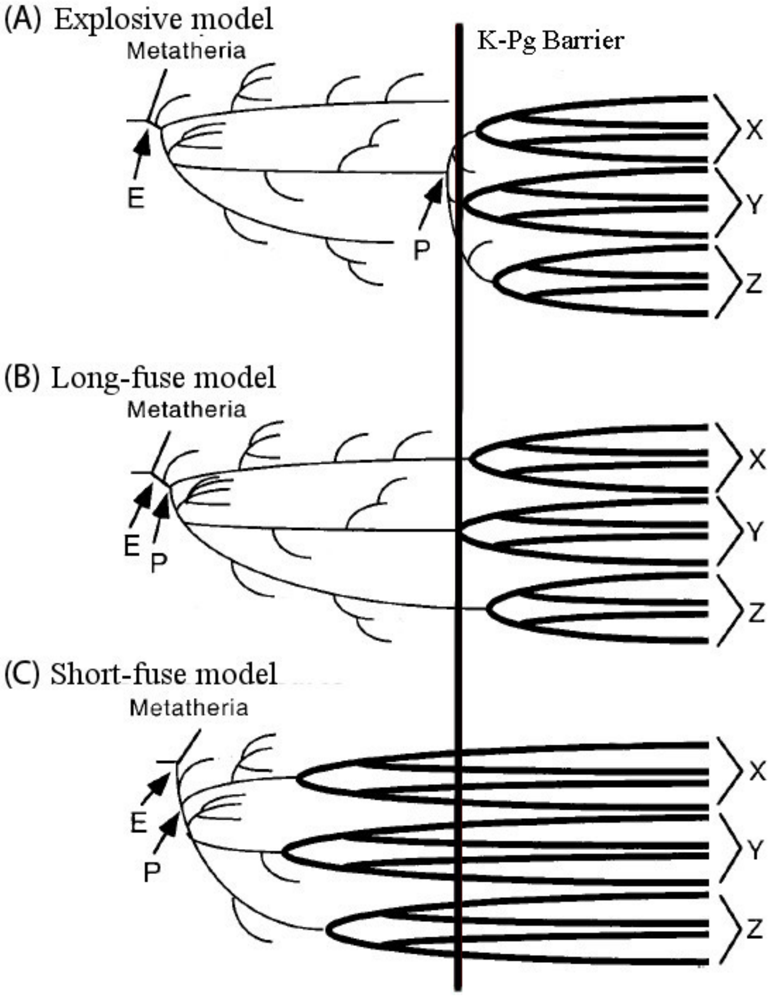


**Figure 3.1:** Theoretical phylogenies representing the alternative hypotheses for the evolution of the placental orders. (**A**) Explosive model; (**B**) Long-fuse model; (**C**) Short-fuse model. Detailed explanation in the text. **X**, **Y**, and **Z** represent 3 hypothetical orders of Placentalia. The vertical line indicates the barrier between the Cretaceous and the Paleogene (K-Pg), at $65.5 \pm 0.3$ Ma. The thicker lines represent the orders crown group. Note: **E**, Eutheria; **P**, Placentalia. Modified from Archibald and Deutschman (2001).

Since 2007, five different phylogenetic hypotheses were proposed (Bininda-Emonds et al., 2007; Meredith et al., 2011; dos Reis et al., 2012; O'Leary et al., 2013; Faurby and Svenning, 2015), each one supporting different models of Placentalia evolution (see Figure 3.1; Bininda-Emonds and Purvis, 2012; Murphy et al., 2012; Goswami, 2012; Yoder, 2013; Springer et al., 2013). Considering this uncertainty about the evolution of the group, we included two phylogenies of placental mammals in our analysis: dos Reis et al. (2012) and Meredith et al. (2011).

The phylogeny of dos Reis et al. (2012, Figure 3.2.A) was constructed using a super matrix framework. This study used an immense amount of data, with 26 fossil calibrations

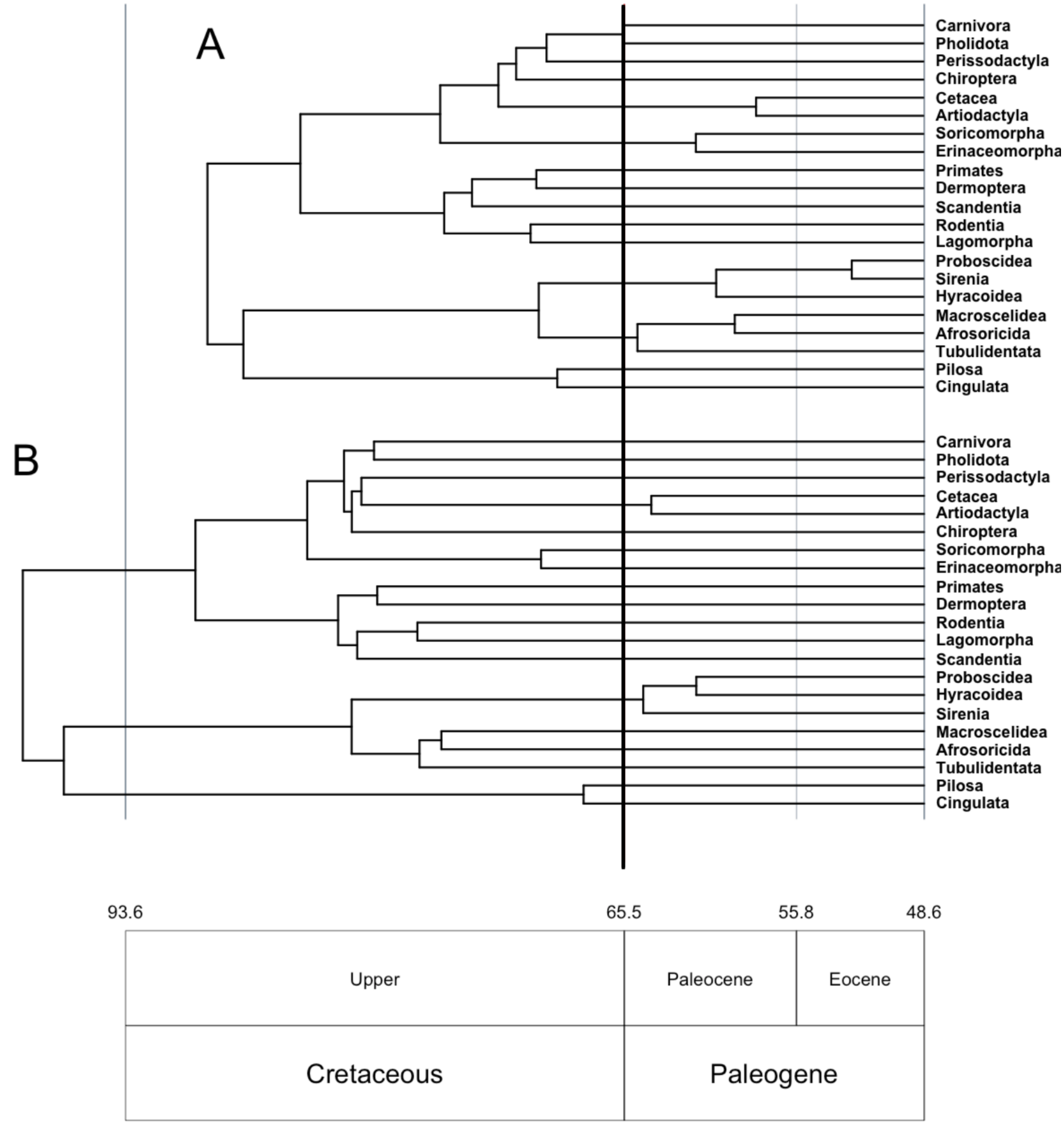


**Figure 3.2:** Phylogenies of the 21 orders of Placentalia. A: phylogeny from dos Reis et al. (2012). B: phylogeny from Meredith et al. (2011). As all the orders appeared before the Lutetian (48.6 - 40.4 Ma), the phylogenies were pruned to better visualization of the phylogenetic relationships. The Cretaceous-Paleogene (K-Pg) barrier is highlighted in black. The numbers represent the time in million years ago.

and more than 14 thousand alignments. The estimated times of divergence indicate a post K-Pg origination of the crown groups of the placental orders - the only exceptions are Xenarthra and Primates. This result supports the explosive model (Figure 3.1.A) and is in accordance with the fossil record (Hedges et al., 1996; Foote et al., 1999; Springer et al., 2003; Goswami, 2012; Yoder, 2013). The phylogeny of Meredith et al. (2011, Figure 3.2.B) was also constructed using a super matrix framework, with 82 fossil calibrations and data from

26 genes of 164 mammalian lineages. According to Meredith et al.'s chronogram most orders originated in the Cretaceous but the intraordinal diversification occurred only after the K-Pg, a scenario in accordance with the long-fuse model (Figure 3.1.B; Luo, 2007; Murphy et al., 2012; Yu et al., 2012; Bininda-Emonds and Purvis, 2012).

At the superordinal level the phylogenies are congruent, with Boreotheria as sister-group of Afrotheria and Xenarthra. At the ordinal level, however, there are three differences in the phylogenetic relationships. Within Laurasiatheria, the phylogeny of dos Reis et al. (2012) exhibits the orders Cetacea and Artiodactyla as sister-group of (Chiroptera (Perissodactyla (Carnivora + Pholidota))), whereas the phylogeny of Meredith et al. (2011) indicates that Carnivora and Pholidota are the sister-group of (Chiroptera (Perissodactyla (Cetacea + Artiodactyla))). Also, within the Euarchontoglires the phylogenetic relationship of the order Scandentia is uncertain. In the phylogeny of dos Reis et al. (2012) Scandentia is the sister-group of Primates and Dermoptera, but in the phylogeny of Meredith et al. (2011) Scandentia is the sister-group of Rodentia and Lagomorpha. Finally, the phylogenetic relationship among three out of the six orders of Afrotheria is controversial. The phylogeny of dos Reis et al. (2012) indicates that Hyracoidea is the sister-group of Proboscidea and Sirenia, whereas the phylogeny of Meredith et al. (2011) exhibits Sirenia as the sister-group of Proboscidea and Hyracoidea.

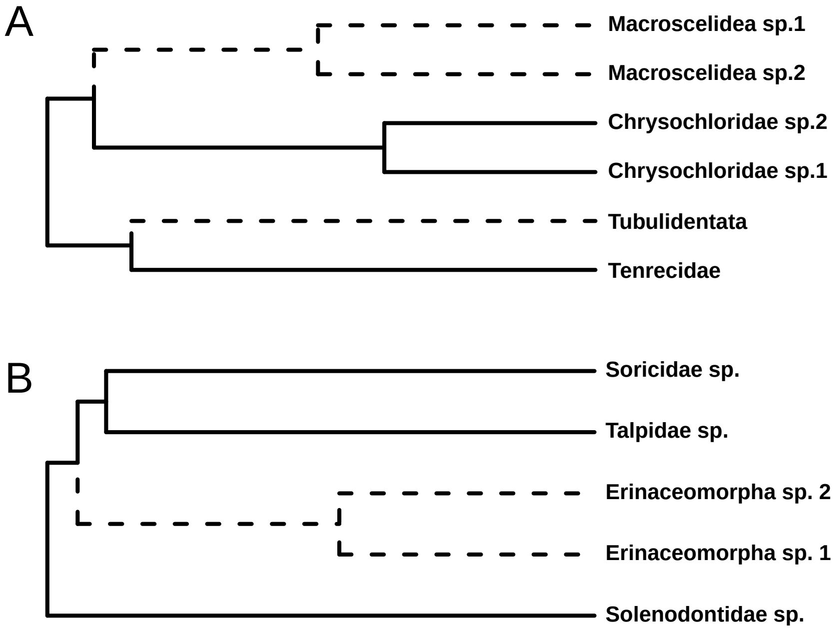


**Figure 3.3:** Phylogenies of the non-monophyletic orders. A: phylogeny showing the polyphyly of the order Afrosoricida (solid line); modified from dos Reis et al. (2012). B: phylogeny showing the paraphyly of the order Soricomorpha (solid line); modified from Meredith et al. (2011).

Furthermore, we investigated the monophyly of each order. As expected, in both phylogenies Artiodactyla is a paraphyletic group. The order Cetacea is a subgroup of Artiodactyla (Gatesy and O'Leary, 2001) and in fact some authors treat these two clades as subgroups of the order Cetartiodactyla. Nevertheless, in this project we considered Cetacea and Artiodactyla as separated orders because the species of these two lineages have completely different life histories and ecologies. In addition, there is one non-monophyletic order in each phylogeny. In the phylogeny of dos Reis et al. (2012) the order Afrosoricida is polyphyletic: two species of the family Chrysochloridae appear as sister-group of Macroscelidea, whereas one species of the family Tenrecidae appears as sister-group of Tubulidentata (Figure 3.3.A). Moreover, in the chronogram of Meredith et al. (2011) the order Soricomorpha is paraphyletic, with one species of the family Solenodontidae appearing as an outgroup (Figure 3.3.B). However, the order Afrosoricidae appears as monophyletic in the phylogeny of Meredith et al. (2011) and Soricomorpha appears as monophyletic in the phylogeny of dos Reis et al. (2012). Besides, in both cases only a few number of species were analyzed (Afrosoricidea: 5.88% of the species; Soricomorpha: 0.7%), this low representation favors the occurrence of long-branch attraction (Bergsten, 2005). Therefore, both orders were treated as monophyletic, with the phylogenetic relationships as shown in Figure 3.2.

## 3.4 Diversity Trajectory

The diversity trajectory of a lineage can be classified in three simple models (Figure 3.4):

- **Expansion model**: assumes that there is no limit for the number of lineages or that the clade is distant from its “carrying capacity” and, therefore, the diversity increases steadily interrupted only by stochastic events that momentarily reduce the diversity (green line in Figure 3.4; Walker and Valentine, 1984; Liow et al., 2010b; Harmon and Harrison, 2015).

- **Saturation (or Logistic) model**: assumes that in the beginning of the diversification process the clade will show a pattern similar to the expected by the expansion model, followed by a phase of reduction in the diversification rate and finally the clade will reach an equilibrium (blue line in Figure 3.4). In the last phase the diversity of the clade would be approximately invariant (i.e., zero rate of diversification), but there would be constant turn-over of lineages (Sepkoski, 1978, 1979, 1984; Alroy, 1996; Morlon et al., 2010).

- **Decline model**: assumes that the clades have a phase of increase and a phase of decrease in diversity (Foote, 2007; Quental and Marshall, 2013), interpolated or not by a phase of equilibrium (red line in Figure 3.4).

In order to determine the trajectory of the 21 orders of placentals, we used the fossil data to estimate the diversity through time with two methods: gap analysis (GAP) and boundary-crosser (BC). Both methods correct for the incompleteness of the fossil record. The GAP consists of estimating the sample probability (i.e., gap stat) of each interval analyzed and then correct the sampled diversity (Paul, 1982). The gap stat for each interval

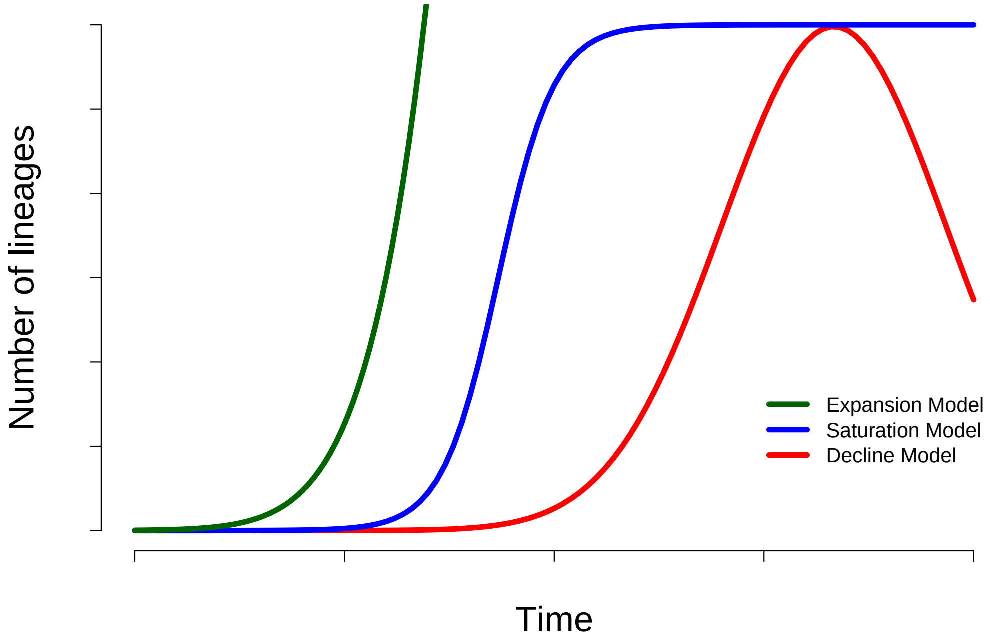


**Figure 3.4:** Models of diversification.

is estimated based only on range-through taxa (i.e., taxa that occur before and after the given interval). The gap stat is calculated as the total number of range-through taxa divided by the number of sampled range-through taxa. Then, the GAP diversity is estimated as the number of sampled taxa divided by the gap stat. This method does not guarantee the coexistence of lineages, especially if the longevity of the lineages is short compared to the duration of the intervals, and it was interpreted as the upper bound estimate of diversity. The BC is estimated based on the number of lineages that cross two consecutive intervals (Foote and Miller, 2007; Quental and Marshall, 2010). Therefore, this method guarantees that the lineages coexisted and it was interpreted as the lower bound estimate.

The diversity methods (i.e., GAP and BC) described above are the simplest ones and it might be difficult to distinguish a significant decline in diversity from the normal variation in the number of genera. In order to improve our classification of diversity trajectory we also estimated the diversification rate (i.e., speciation rate - extinction rate) of each order calculated with the instantaneous per-capita rates method (perCapita; Foote, 2000). Foote (2000) divided the taxa of each interval in four classes: $N_{FL}$ is the number of taxa confined to the given interval (i.e., singletons); $N_{bL}$ is the number of taxa that appeared in older intervals and last occur in the given interval; $N_{Ft}$ is the number of taxa that first appear in the given interval and also occur in the subsequent intervals; $N_{bt}$ is the number of range-through taxa. The rate of origination ($p$) is:

$$p = -\frac{ln(N_{bt}/(N_{Ft}+N_{bt}))}{\Delta t};$$

and the extinction rate ($q$) is:

$$q = -\frac{ln(N_{bt}/(N_{bL} + N_{bt}))}{\Delta t},$$

where $\Delta t$ is the duration of the given interval. Then, the perCapita diversification rate is estimated subtracting the extinction rate ($q$) from the origination rate ($p$). This method was also developed to deal with the biases and incompleteness of the fossil record and can be used to infer the recent diversification dynamics (e.g., the last 5 million years). We analyzed the diversification rates in the three stages of the Pliocene: Zanclean (5.332 - 3.600 Ma), Piacenzian (3.600 - 2.588 Ma), and Gelasian (2.588 - 1.806 Ma). The Pleistocene (1.806 - 0.012 Ma) was not considered because its stages (i.e., Lower, Middle, and Upper Pleistocene) have really short durations (average duration = 0.598 My), which could generate biased rates estimates. By focusing in the stages of the Pliocene we captured the more recent diversification dynamics of the orders. This investigation of the dynamics in the recent allows the comparison with the results based on the diversity metrics, which consider the whole range of the order.

Each order of Placentalia was classified into Decline, not-decline, or inconclusive. For the BC and GAP methods, the classification was made comparing the maximum estimated diversity from the fossil record with the number of genera in the present (based on Wilson and Reeder, 2011). The Decline was inferred in the cases where the diversity in the past was higher. For the perCapita method, considering only the more recent diversification dynamics, the Decline was inferred in the cases where the weighted average of the diversification rates during the Pliocene was negative. The Expansion and Saturation models were grouped under not-decline. Given the incompleteness of the fossil record, one cannot estimate properly the maximum number of lineages, which makes it extremely difficult to distinguish between the models of Expansion and Saturation. Moreover, we cannot differentiate an Expansion model from a Saturation model based only on the rates of diversification, as positive rates estimates might be consistent with both models (see discussion in section 5.1). On the order hand, the inference of Decline, the model we are interested in, is more robust: if one can infer decline of diversity based on the fossil record despite its incompleteness, then the diversity decline must have occurred.

The three analyzes (i.e., GAP, BC, and perCapita) were repeated for the "stg1" dataset and the 1,000 randomizations of "stg2". An order was considered in Decline when the decline of diversity was inferred in the "stg1" dataset and in at least 95% of the randomizations of the "stg2" dataset. Also, we classified as not-decline the orders in which the decline of diversity was not inferred in the "stg1" dataset and was only inferred in 5% or less of the randomizations of the "stg2" dataset. The orders that did not match any criteria were considered inconclusive. Therefore, we had three definitions of the Decline for each of the 21 orders of Placentalia: gap-analysis, boundary-crosser, and the per-capita rates of diversification.

## 3.5 Body Size

The body mass was used to represent the body size of the species. The body mass of extant species was gathered from the “EltonTraits database” (Figure 1.1; Wilman et al., 2014), which is the most complete global species-level compilation of body mass available and contains information for 5,066 species of extant placental mammals ($\approx$ 94.53% of the total, Wilson and Reeder, 2011). Given the high variability in body mass, all estimates were log transformed. In order to investigate the effect of body mass on the diversification dynamics, we estimated the body mass of each order of Placentalia. The method used was the harmonic mean:

$$H = \left( \frac{1}{n} * \sum_{i=1}^{n} x_i^{-1} \right)^{-1},$$

where **n** is the number of elements and $x_i$ is the element **i**. The harmonic mean is more suitable than the arithmetic mean because it reduces the effect of outliers (Cooper and Purvis, 2010) and better represents the body mass of the whole order. This becomes more evident in the orders with many outliers (e.g., Carnivora and Rodentia), in which the arithmetic mean is closer to the outliers while the harmonic mean is similar to the median (Figure 3.5).

The association between the decline of diversity and the body size may be biased if the size of a lineage influences its probability of preservation. If a bigger lineage has a higher probability of fossilizing than a smaller lineage, then the Decline will be preferentially detected in the bigger lineages. Such a scenario might generate a significant correlation between the body size and the decline of diversity even when there is no true association between the variables. In order to assess this possible bias we estimated the frequency ratio (freqRat; Foote and Raup, 1996), an estimative of the sampling probability in the fossil record. This metric is estimated as:

$$freqRat = \frac{{f_2}^2}{f_1 * f_3},$$

where $f_1$, $f_2$, and $f_3$ are the number of taxa observed in one, two, and three intervals, respectively. The method assumes that the intervals have fairly similar lengths and taxa sampling works similar to a Poisson process. The freqRat varies between one (perfect sampling) and zero. Values higher than one indicate violation of the assumptions. This method is available in the function “freqRat” in the package “paleotree” of R (Bapst, 2012). This analysis was conduct only in the “stg1” dataset, which represents the best data from the fossil record. The sampling probability was, then, correlated with the body mass to investigate preservation biases related to body size.

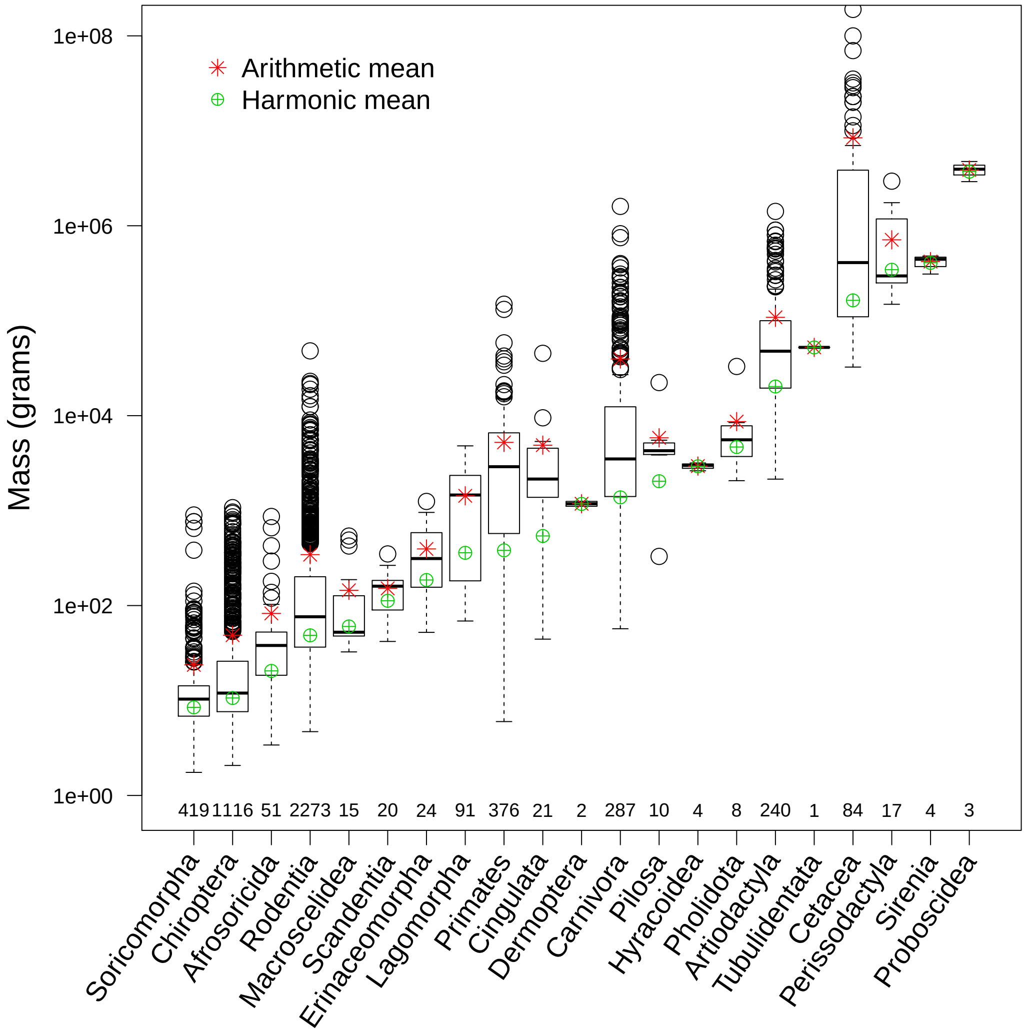


**Figure 3.5:** Distribution of body mass of the 21 orders of Placentalia. The arithmetic mean is indicated by the red asterisk, the harmonic mean in indicated by the green dot. The black circles represent outliers. The horizontal lines represent the $1^{st}$, $2^{nd}$, and $3^{rd}$ quartiles. The upper and lower whiskers indicate, respectively, the $1^{st}$ quartile plus the inner quartile range and the $3^{rd}$ quartile minus the inner quartile range. The numbers above the x-axis indicate the number of species analyzed for each order. The masses are based on the "EltonTraits database" (Wilman et al., 2014).

## 3.6 Morphological Disparity

The morphological disparity of each order of Placentalia was calculated using the body mass of the extant species ("EltonTraits database"; Wilman et al., 2014). The disparity was estimated using two metrics: mean pairwise distance (MPD) and mean nearest neighbor distance (MNND). The MPD is defined as the sum of the Euclidean distances in morphospace between all possible pairwise combinations divided by the total number of combinations (Ciampaglio et al., 2001). This metric is similar to the variance, but it is more robust to compare samples of different size (Ciampaglio et al., 2001). The MNND can be interpreted as a special case of the MPD metric, in which for each species only the shortest distance in morphospace is considered (Ricklefs and Miles, 1994, chap. 1). Each metric indicates different aspects of the morphospace occupation. While MPD indicates the variation in the occupancy of the morphospace, MNND indicates how clumped the species are in the morphospace. Given the variability in body mass across the orders of Placentalia (Figure 3.5), we have normalized both metrics, dividing the estimated disparity metric by the harmonic mean of each order. The order Tubulidentata is monospecific and was excluded from this analysis.

## 3.7 Extinction Risk

The extinction risk was assessed based on the "IUCN Red List of Threatened Species" (Red List; `http://www.iucnredlist.org/`). In order to study the relation between the decline of diversity inferred from the fossil record and the risk of extinction of the extant species, we estimated the extinction risk for the 21 orders of Placentalia using the proportion of extinct species (i.e., extinct and extinct in the wild) and species in the threatened categories (i.e., critically endangered, endangered, and vulnerable) - for a similar approach see Purvis et al. (2000). To make this approach more similar to the fossil record analysis, we estimated the proportion of species in risk of extinction for each genera (Barnosky et al., 2011). Genera with at least 50% of species at risk were considered endangered and were assigned a value of one. Genera with less than 50% of species at risk were considered not-endangered and were assigned a value of zero. Then, we estimated the mean value for each order, which represents the percentage of extant genera at risk of extinction, and calculated the correlation with the Decline.

## 3.8 Phylogenetic Signal

Phylogenetic comparative methods allows one to test whether there is a phylogenetic signal (i.e., the tendency of a lineage being more similar to its sister-group than to a lineage drawn randomly from the phylogeny) as well as to correctly test evolutionary hypotheses. There are several phylogenetic comparative methods (Nunn, 2011), each one developed to analyze specific types of data. The method of Fritz and Purvis (2010) was developed to analyze binary traits and we used it to evaluate the phylogenetic signal of the Decline model. This method estimates the changes in nodal values along a phylogeny (D). The empirical value of D is then compared to two null distribution simulated under different scenarios: phylogenetic randomness and brownian threshold. The former consists of randomizing the traits values among the tips of the phylogeny, whereas the latter consists of simulating a trait evolving under a Brownian motion model (Diniz-Filho, 2000) and then converting it to a binary trait using a threshold that maintains the relative prevalence of the observed trait. The method is available with the function "phylo.d" in the package "caper" of R (Orme et al., 2013).

Given their shared evolutionary history, in general, closely related lineages cannot be considered independent observations and need specific statistical methods (Garland et al., 1999). On the other hand, one should not use phylogenetic methods for the analysis of traits that do not have a significant phylogenetic signal (Björklund, 1997; Freckleton, 2009). Therefore, we tested for phylogenetic signal for the body size (section 3.5), the morphological disparity (section 3.6), and the extinction risk (section 3.7) before analyzing their correlation with the Decline model (section 3.9). There are several measures of phylogenetic signal developed to deal with continuous traits (Diniz-Filho et al., 2012). The most commonly used model based approaches are the Pagel's $\lambda$ (Pagel, 1999) and Blomberg's $K$ (Blomberg et al., 2003). Both metrics are highly correlated (Diniz-Filho et al., 2012). Nevertheless, a simulation study conducted by Münkemüller et al. (2012) indicates that Pagel's $\lambda$ was the least affected by the number of tips and that Blomberg's $K$ showed a much higher type II error (i.e., false negative) for intermediate strength of the Brownian motion model. Thus, in this study we used only Pagel's $\lambda$.

$\lambda$ is a scaling parameter for the correlations between tips estimated with maximum likelihood. Higher values of $\lambda$ indicate stronger phylogenetic signal and $\lambda$ equal one represents a scenario in line with the Brownian motion model. The estimated value is then compared against a scenario where $\lambda$ equals zero (i.e., no phylogenetic signal) using likelihood ratio test. This metric allows one to incorporate the intraclade variation, hence we calculated the standard error of the traits for each order of placentals. This method is implemented in the function "phylosig" in the package "phytools" of R (Revell, 2012).

## 3.9 Correlations

To investigate possible explanations for the variation in the diversification trajectories of the lineages of Placentalia, we correlated the body size (section 3.5), the morphological disparity (section 3.6), and the extinction risk (section 3.7) with the Decline model results. The correlations were estimated taking into consideration only the orders in Decline and not-decline. The orders considered inconclusive (see section 3.4) were removed from the analyses.

In order to evaluate the sensitivity of our results to the characterization of the Decline, the correlation analyzes were repeated including the inconclusive orders as Decline and not-decline. We used the Bonferroni correction to deal with the multiple comparisons.

For the cases with a significant correlation with the Decline model, it is possible to investigate the trait's effect on the rates of diversification. The rates of origination and extinction control the trajectory of a lineage, hence if a trait is correlated with the decline of diversity it is expected that the same trait will have a significant effect on the diversification rates. Therefore, we correlated the significant traits with the per-capita rates of origination and extinction (described in section 3.4) for the whole range of each order. For this analysis we only considered the orders for which it was possible to estimate the per-capita rates in at least 50% of their geological stages. The rates of diversification in this analysis that consider the whole range of the orders, will be referred to as footeRates in order to avoid confusion with the perCapita method of characterization of Decline (see section 3.4).

For the traits with a significant phylogenetic signal, the correlation analyzes were made using generalized estimating equations (GEE; Paradis and Claude, 2002). This method constructs a variance-covariance matrix based on the phylogeny and uses it to correct for the non-independence of the lineages. The GEE method is available with the function "compar.gee", in the package "ape" of R (Paradis et al., 2004). For the traits that do not have a significant phylogenetic signal, we used the Point Bi-Serial Correlation. This correlation is a statistic used to analyze the strength of the association between a binary variable (e.g., decline of diversity) and a continuous variable (e.g., body mass). The Point Bi-Serial Correlation Coefficient is mathematically equivalent to the Pearson Bivariate Correlation Coefficient, thus the correlations were tested using the function "cor.test".

# 4 Results

The complete dataset contains 108,523 fossil occurrences (68,008 from PBdata and 40,515 from NOW) and 4,280 genera. The majority of the occurrences have a good resolution. The average occurrence duration is 3.52 My (Appendix I top) and 83.84% of the occurrences are assigned to one or two stages (Appendix I bottom). In the more restrictive case, considering only occurrences assigned to one stage (i.e., “stg1”) there are 53,087 fossil occurrences, distributed among 3,199 genera (Table I). In the dataset containing occurrences within 2 stages or less (i.e., “stg2”) the number of fossil occurrences, after removing the possible duplicated entries, drops to 11,315 which are distributed among 4,003 genera (Table I). The average genera longevity increases from 5.15 My in the “stg1” dataset to 6.26 My in the “stg2” (Appendix II). There is a difference of more than 800 genera between the two datasets and these new genera in average occur in 2.26 stages, encompassing 4.23 My (Appendix II). The raw curves of diversity (i.e., not corrected to the imperfections of the fossil record) are available in Appendix VII.

The analysis of the diversity through time (Figure 4.1) indicates that a considerable amount of the orders of placentals show evidence of Decline. Considering the boundary-crosser method (BC), there are 6 orders in decline of diversity in the “stg1” dataset and this number increases to 12 orders in the analysis of the 1,000 randomizations of the “stg2” (Table 4.1). As expected, all the orders considered in decline of diversity with the BC method were also considered in Decline with the gap-analysis (GAP). In total GAP yelded 15 and 17 orders in Decline for the analysis of the “stg1” dataset and the randomizations of the “stg2”, respectively (Table 4.1). The characterization of Decline and not-decline was highly congruent among the different metrics. The orders Cetacea, Hyracoidea, Perissodactyla, Proboscidea, Sirenia, and Tubulidentata were considered to be in decline of diversity in all diversity analyzes. On the other hand, there was no indicative of Decline in any of the four metrics for the orders Afrosoricida, Chiroptera, and Scandentia.

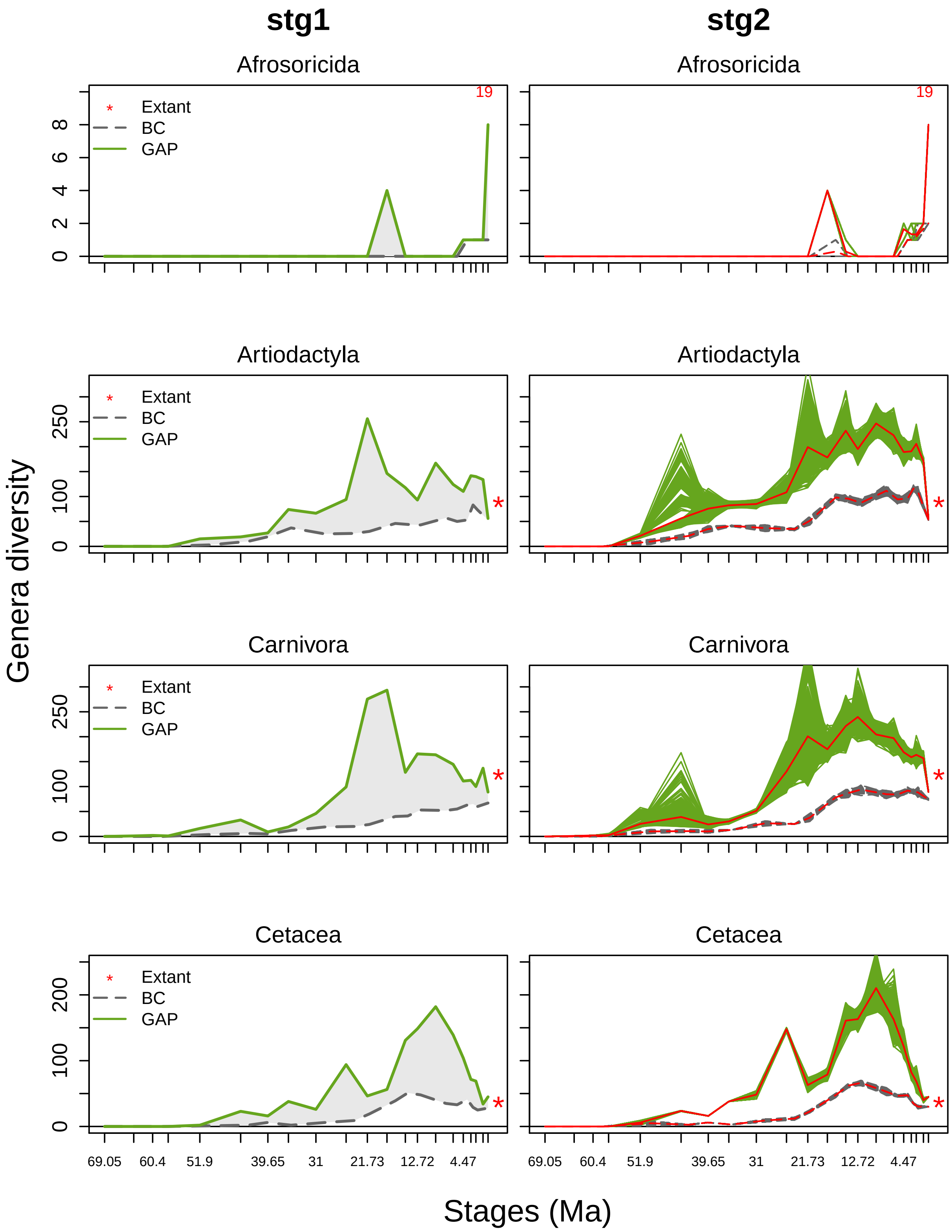


**Figure 4.1:** Diversity through time for the 21 orders of Placentalia. Left: estimates based on "stg1" dataset. Right: estimates based on the 1,000 randomizations of "stg2"; the red solid and dashed line is the average diversity. Solid green line is gap-analysis diversity estimate; dashed black line represent the boundary crosser diversity estimate. Red point and red numbers represent the extant genera diversity according to Wilson and Reeder (2011). Note: the y-axis vary among orders.

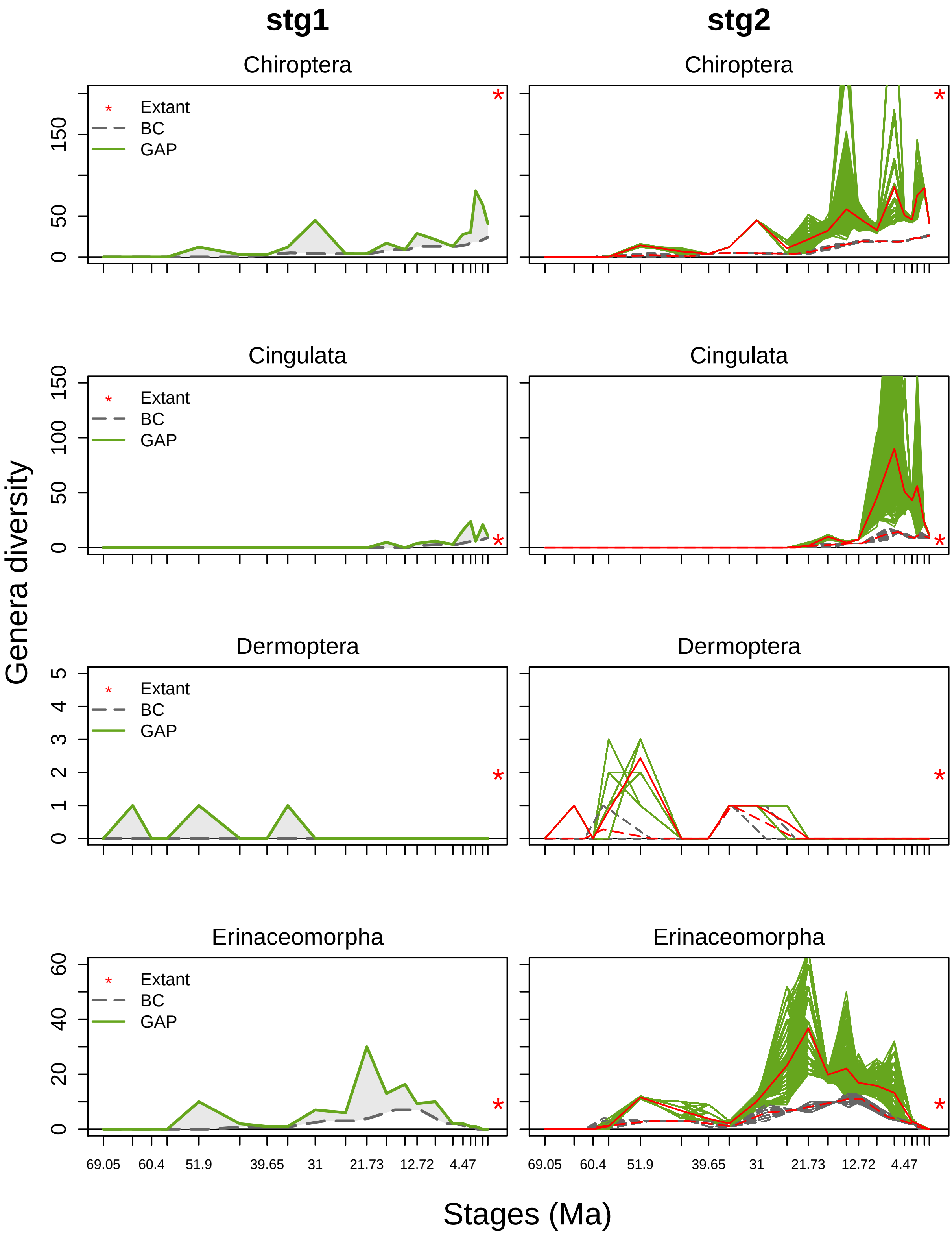
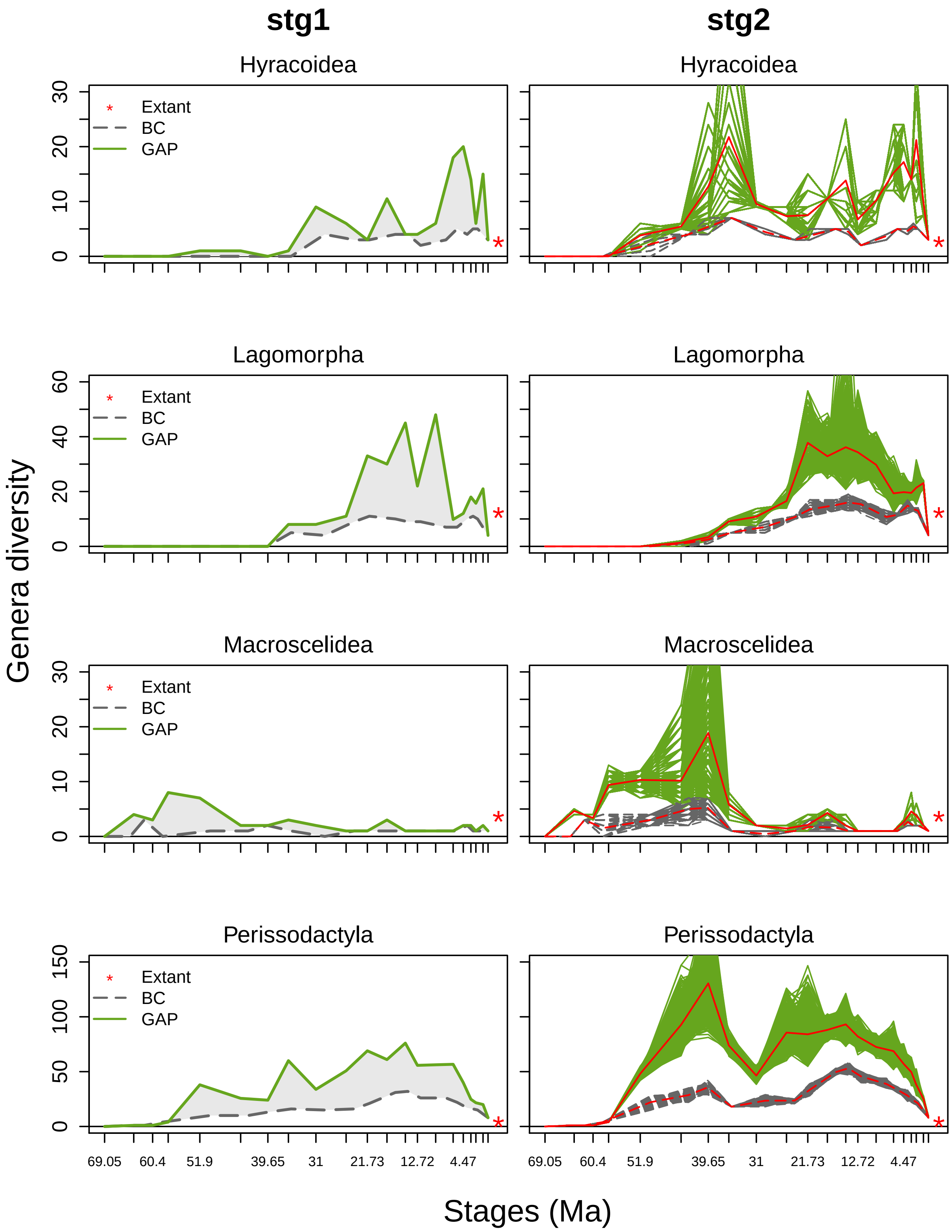


Figure 4.1 cont.



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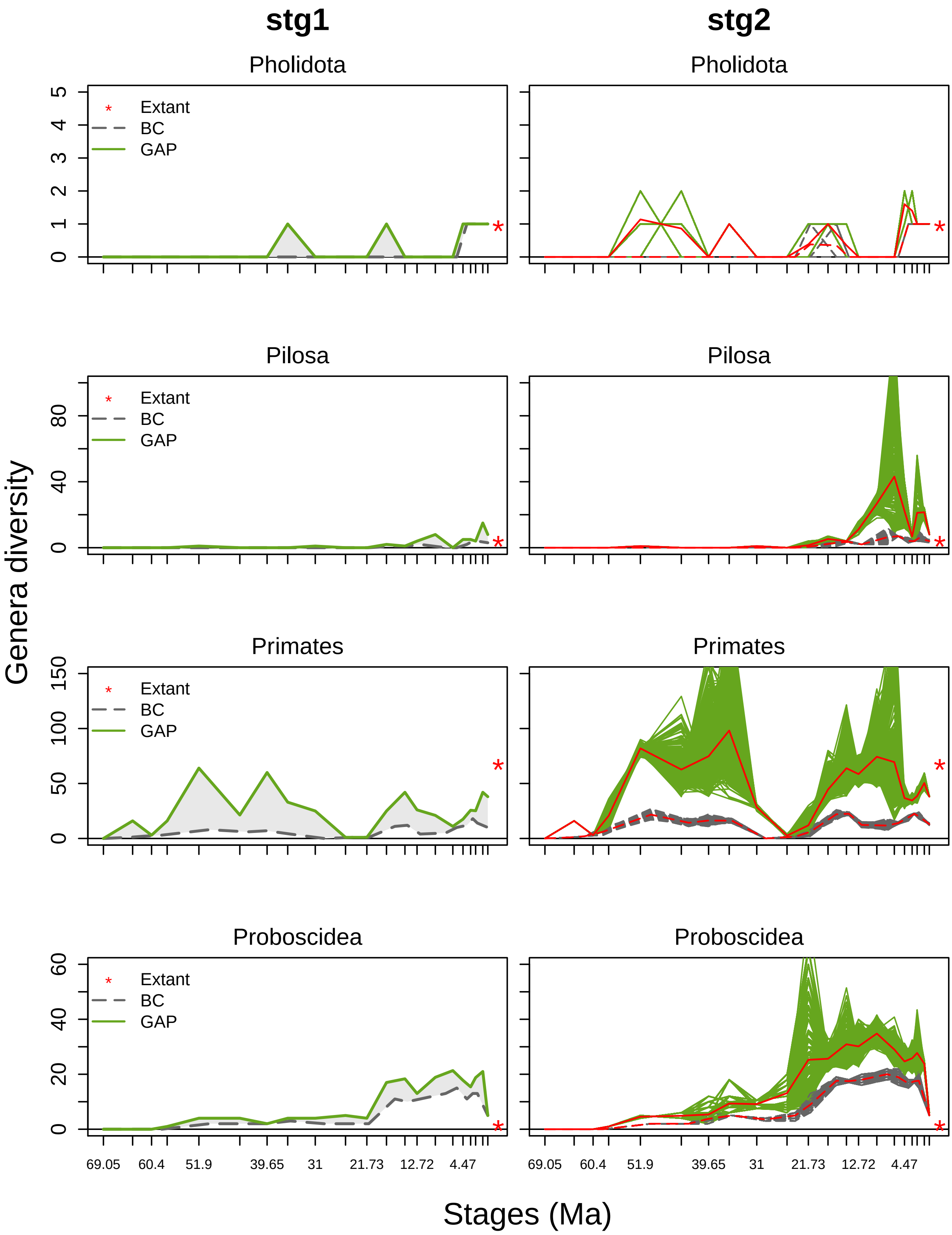

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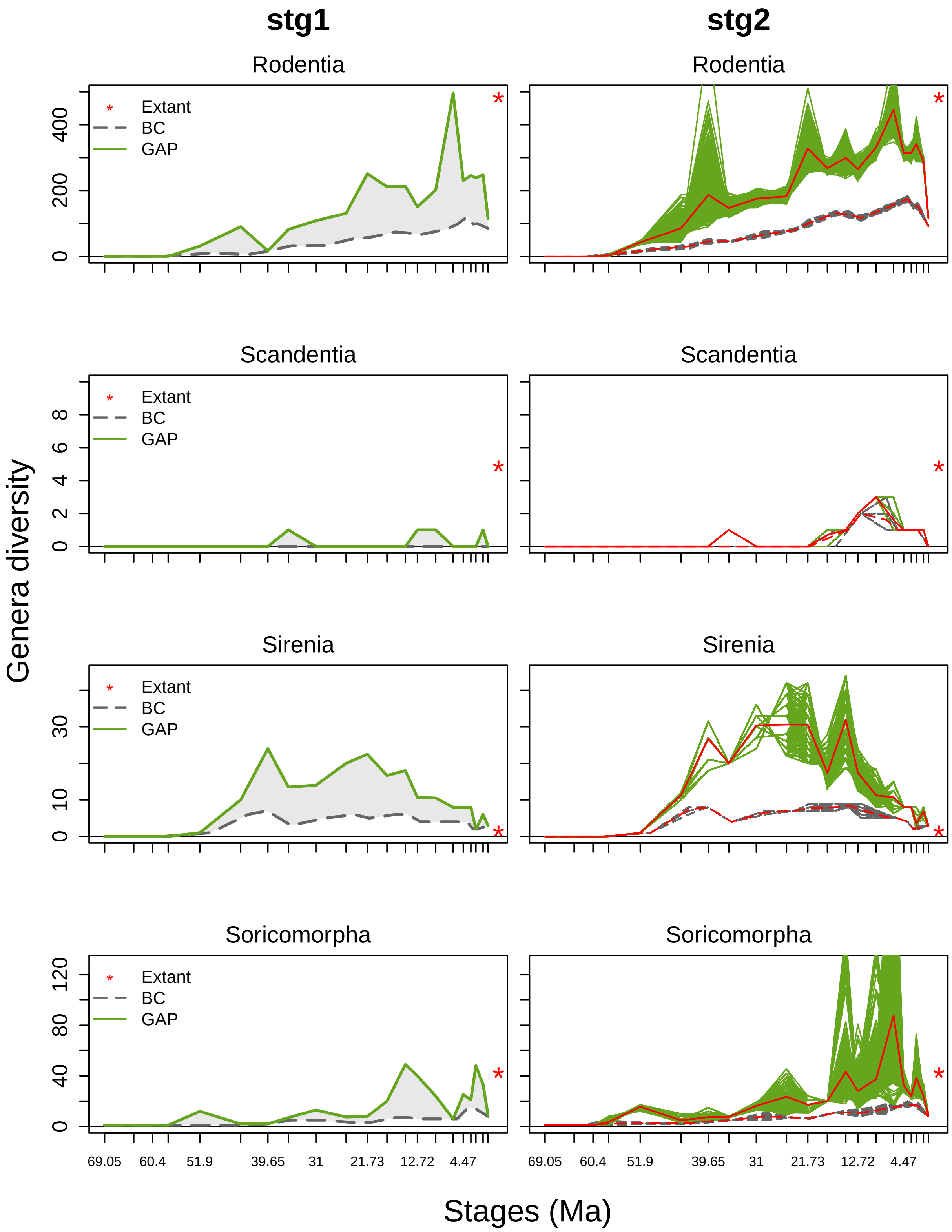

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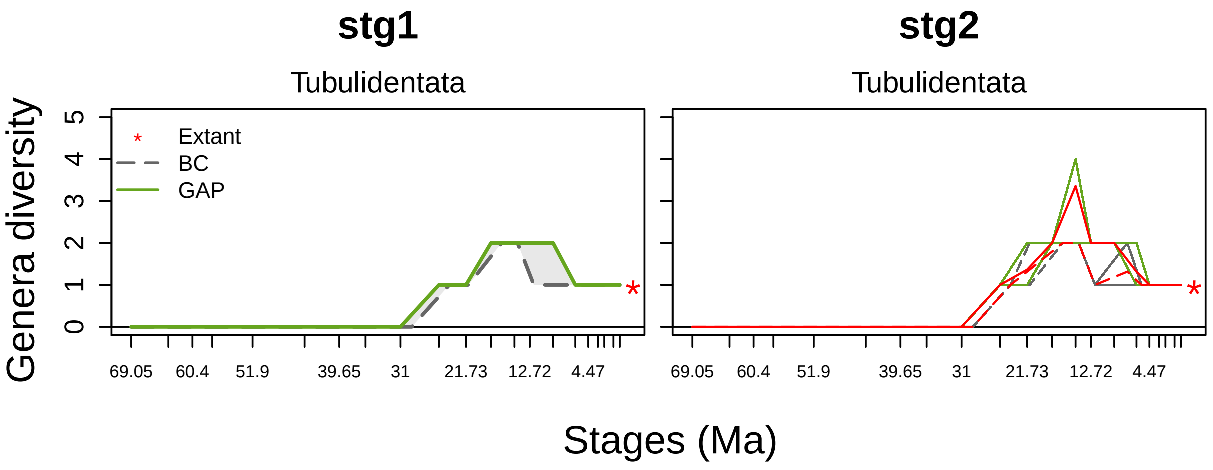


Figure 4.1 cont.

The analysis of the rates of diversification during the Pliocene (i.e., perCapita method) indicates a different scenario (Figure 4.2). In the analysis of the "stg1" dataset, only 5 orders have a signal of recent decline in diversity (Table 4.2). Additionally, the analysis of the 1,000 randomizations of "stg2" indicates that 6 orders are in recent Decline (Table 4.2). In total 10 orders have no indication of recent decline of diversity in both datasets, namely: Afrosoricida, Artiodactyla, Chiroptera, Hyracoidea, Lagomorpha, Macroscelidea, Pholidota, Primates, Scandentia, and Tubulidentata.

**Table 4.1:** Comparison of the peak genera diversity in the fossil record and the extant diversity for the 21 orders of Placentalia. "BC" and "GAP" are the maximum diversity estimates for the boundary-crosser and gap analysis methods, respectively. "stg2" indicates the mean diversity estimate based on the 1,000 randomizations of "stg2"; the number in parenthesis indicates the percentage of randomizations that were considered in decline of diversity. "Extant" is the extant genera diversity according to Wilson and Reeder (2011). The cases where Decline was inferred are highlighted in bold.

| Order | stg1.BC | stg2.BC | stg1.GAP | stg2.GAP | Extant |
|---|---:|---:|---:|---:|---:|
| Carnivora | 67 | 94.9 (0) | **293.3** | **254.5 (100)** | 128 |
| Pholidota | 1 | 1 (0) | 1 | **2 (100)** | 1 |
| Perissodactyla | **32** | **53.1 (100)** | **76** | **131.5 (100)** | 6 |
| Chiroptera | 24 | 26 (0) | 81 | 103.2 (1.9) | 202 |
| Cetacea | **51** | **66.4 (100)** | **182** | **210.8 (100)** | 40 |
| Artiodactyla | 83 | **116.4 (100)** | **256** | **253.7 (100)** | 93 |
| Soricomorpha | 15 | 17.9 (0) | **49** | **92.5 (96.2)** | 44 |
| Erinaceomorpha | 7 | **11.6 (89.6)** | **30** | **38.6 (100)** | 10 |
| Primates | 18 | 23.3 (0) | 64 | **113.4 (100)** | 69 |
| Dermoptera | 0 | 1 (0) | 1 | **2.5 (52.6)** | 2 |
| Scandentia | 0 | 2.1 (0) | 1 | 3 (0) | 5 |
| Rodentia | 120 | 174.4 (0) | **496.1** | 446.6 (12) | 489 |
| Lagomorpha | 11 | **16.6 (100)** | **48** | **43.2 (100)** | 13 |
| Proboscidea | **15** | **20.2 (100)** | **21.3** | **38 (100)** | 2 |
| Sirenia | **7** | **8.7 (100)** | **24** | **37 (100)** | 2 |
| Hyracoidea | **5** | **7 (100)** | **20** | **30.1 (100)** | 3 |
| Macroscelidea | 3 | **5.7 (94.5)** | **8** | **20.2 (100)** | 4 |
| Afrosoricida | 1 | 2 (0) | 8 | 8 (0) | 19 |
| Tubulidentata | **2** | **2 (100)** | **2** | **3.4 (100)** | 1 |
| Pilosa | 4 | **7.4 (100)** | **15** | **50 (100)** | 5 |
| Cingulata | 9 | **14.6 (100)** | **24** | **103.2 (100)** | 9 |

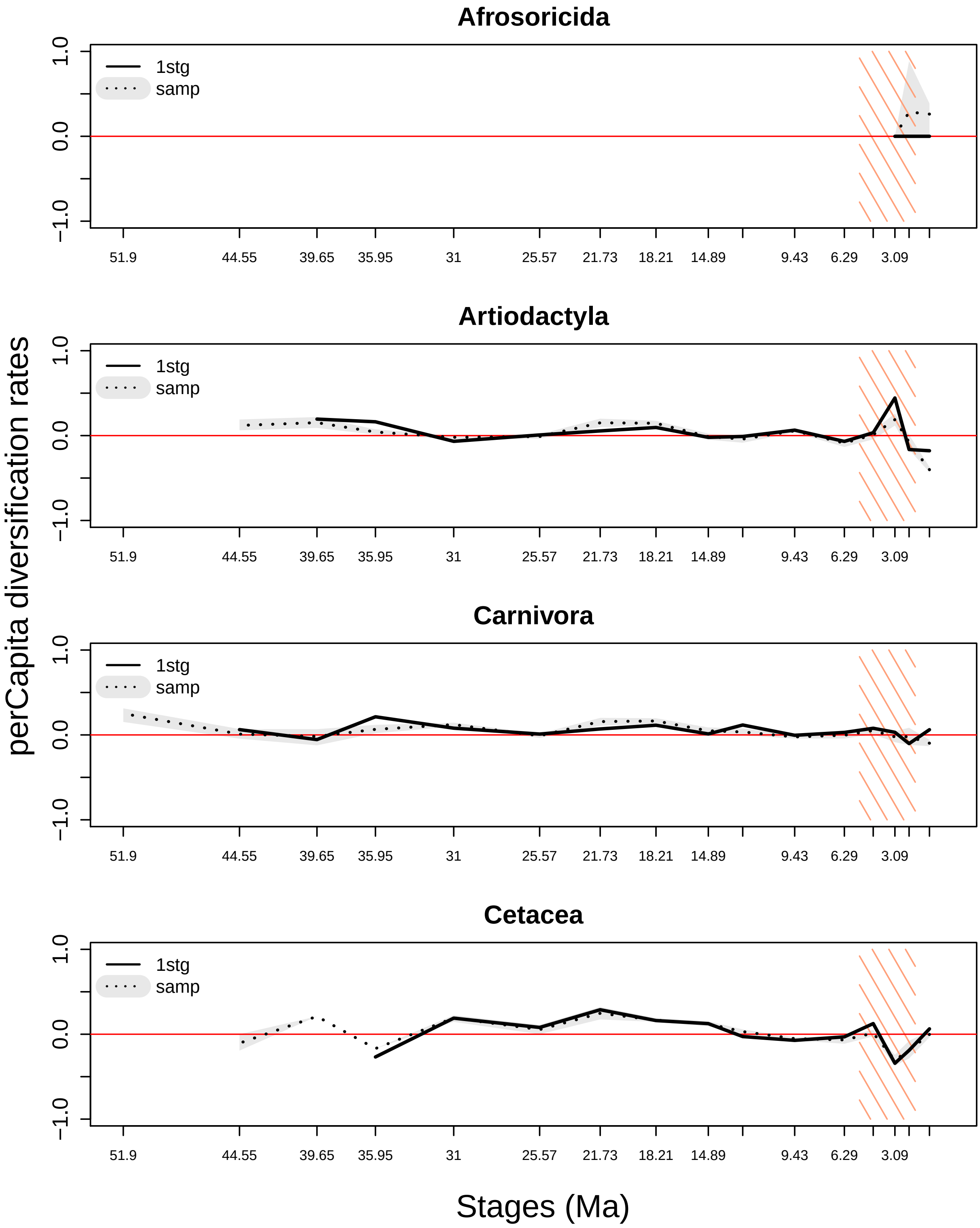


**Figure 4.2:** Rate of diversification (origination – extinction) for the 21 orders of Placentalia. Values below the red line represent negative diversification rate. Dotted line: estimates based on "stg1" dataset. Solid line: estimates based on the 1,000 randomizations of "stg2"; the grey area contains 95% of the estimates. The shaded area represents the Pliocene (5.332 - 1.806 Ma). Note: Due to the scarcity of data the order Dermoptera do not have any rate estimate.

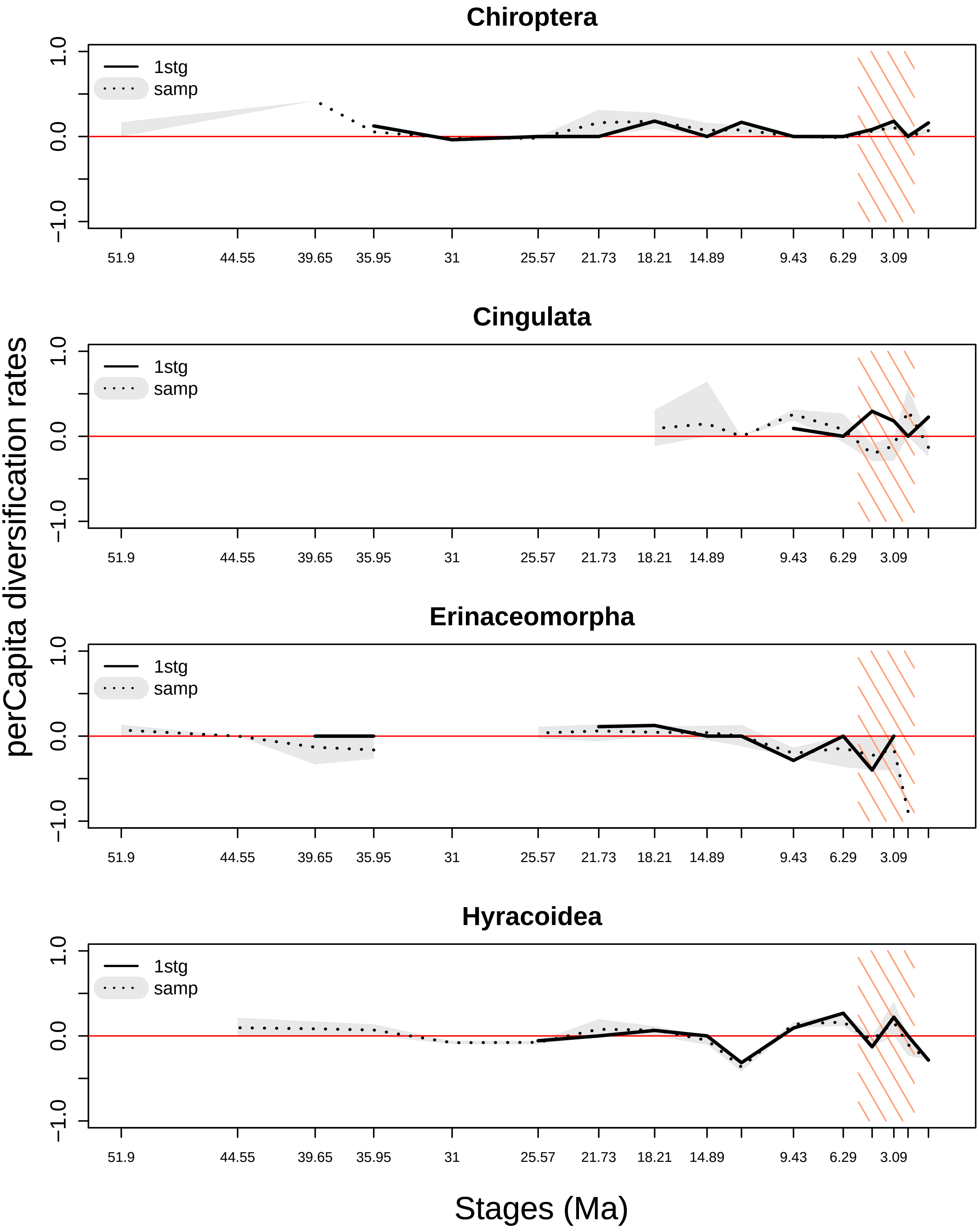
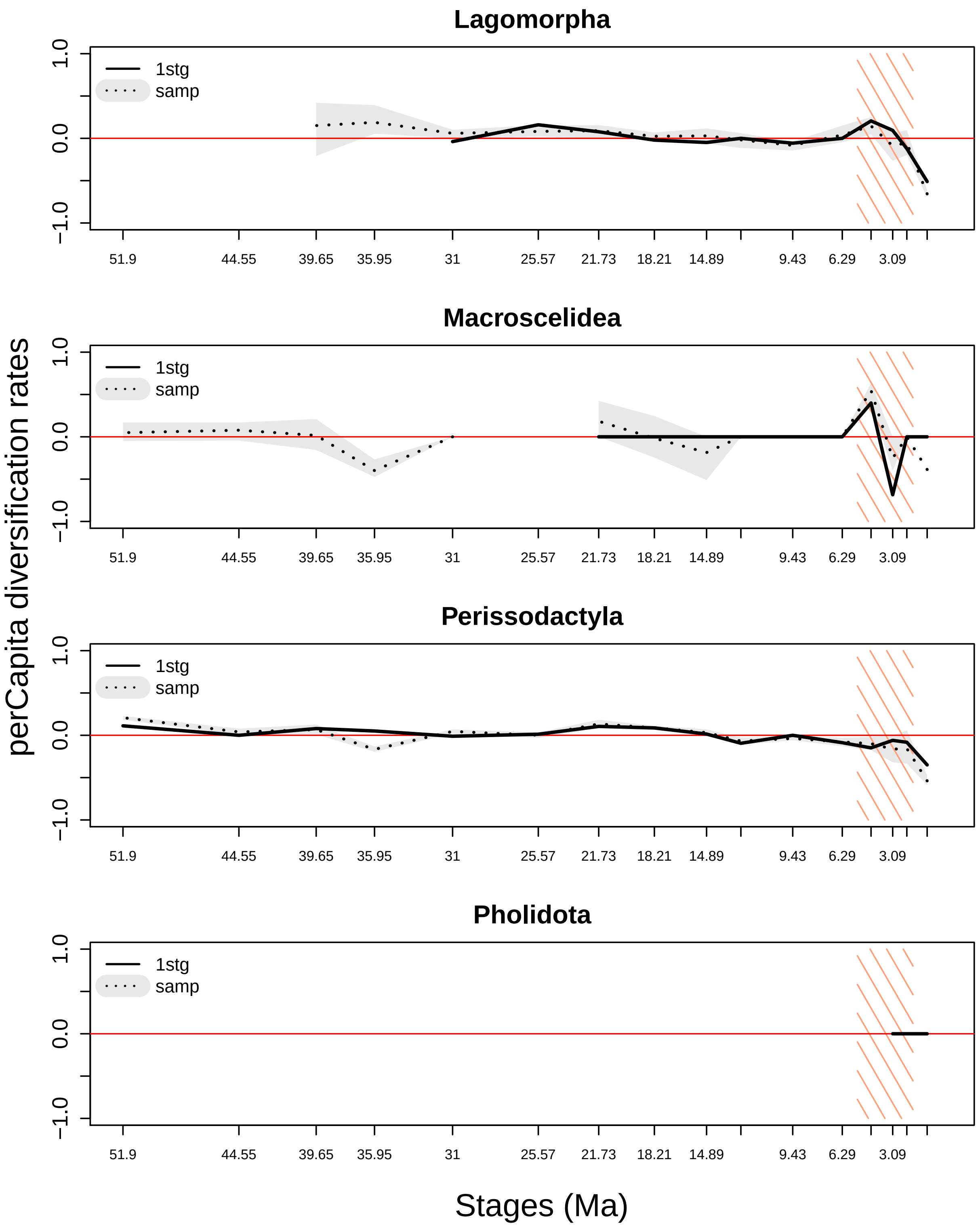


Figure 4.2 cont.



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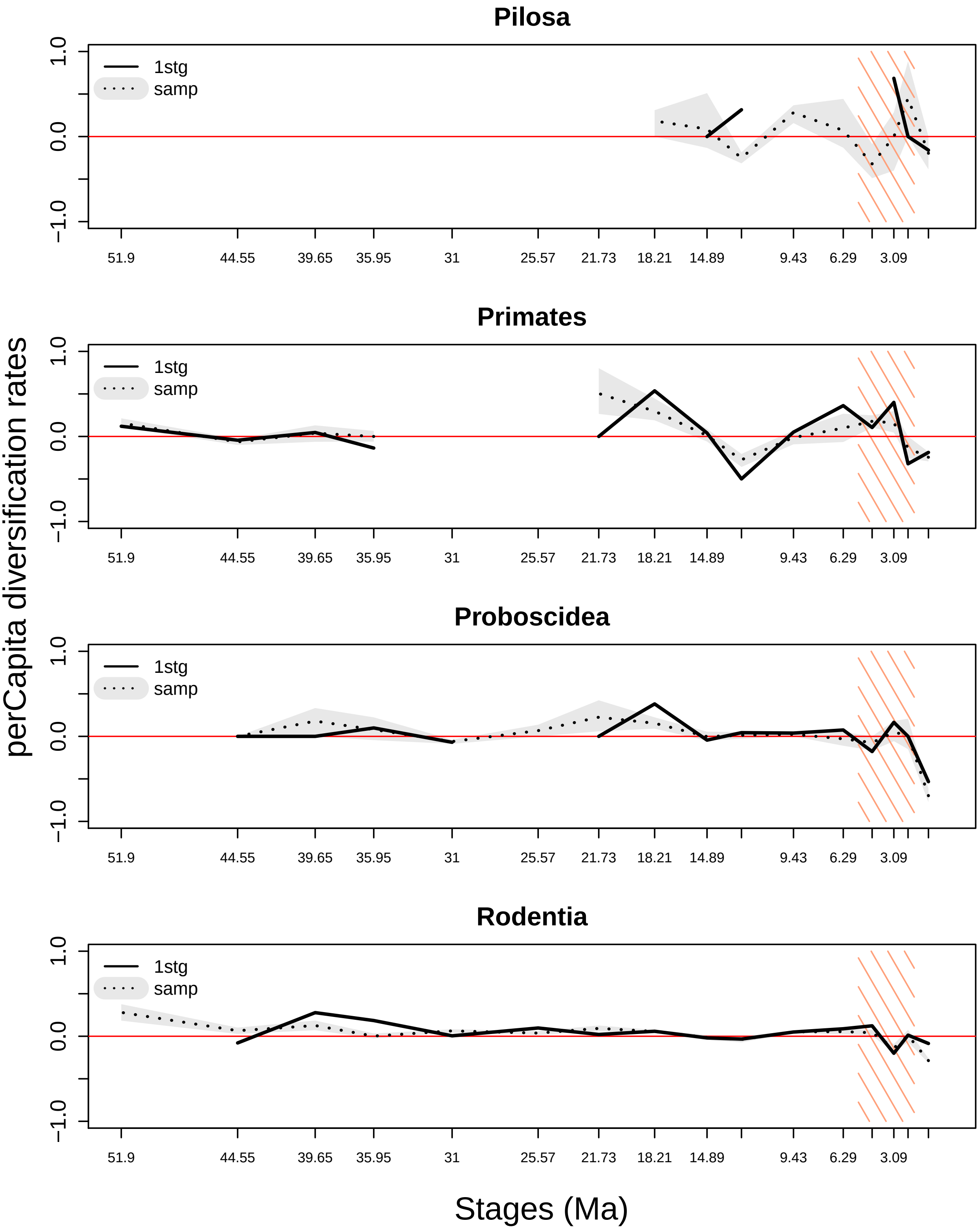

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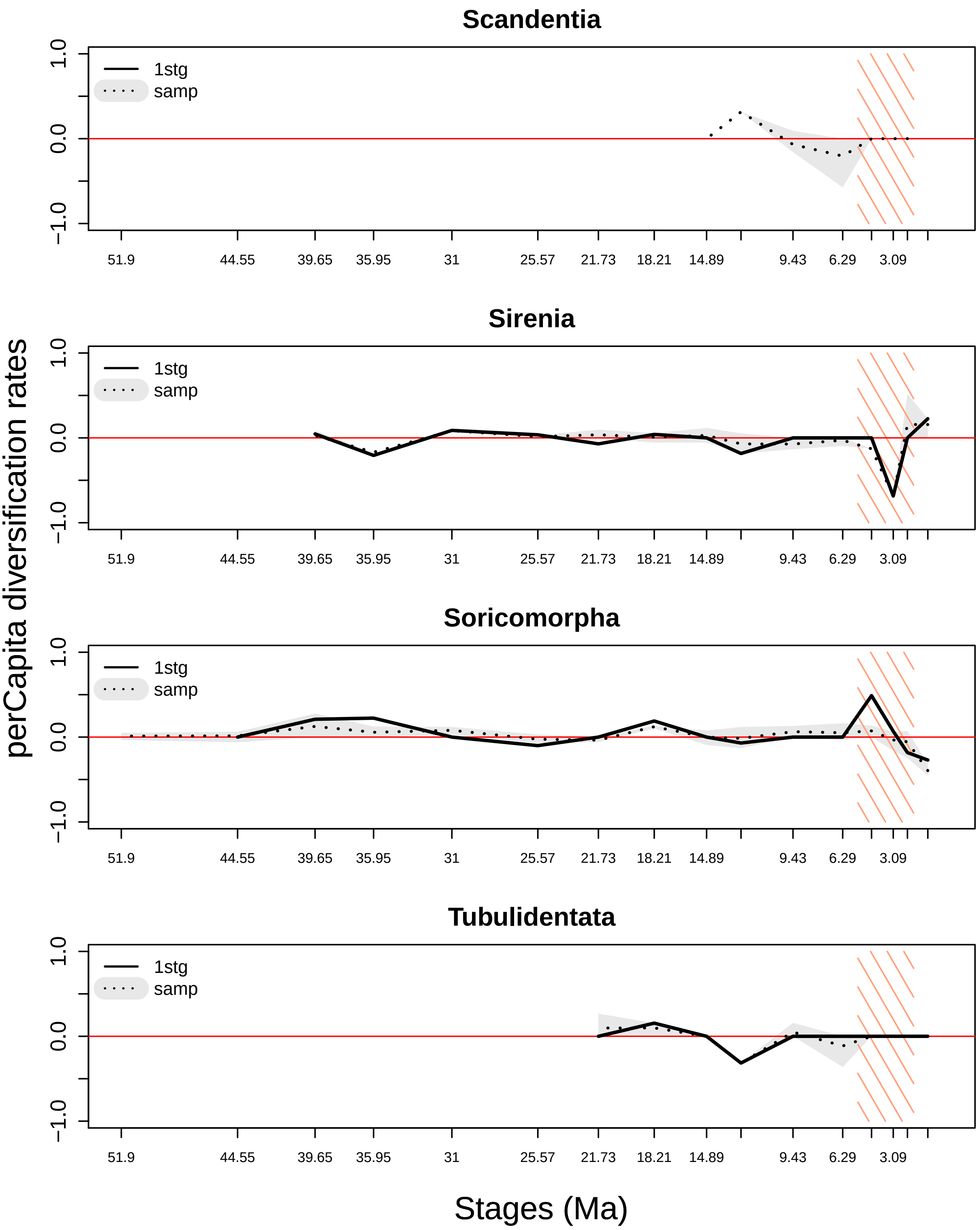

Figure 4.2 cont.

**Table 4.2:** Average diversification rates for the Pliocene (5.332 - 1.806 Ma). The cases where the rate estimate was negative are highlighted in bold. "stg1" and "stg1.r" represent, respectively, inference of Decline and estimate diversification rate for the "stg1" dataset. "stg2" and "stg2.r" represent, respectively, percentage of randomizations in Decline and mean diversification rate estimate for the 1,000 randomizations of "stg2".

| Order | stg1 | stg1.r | stg2 | stg2.r |
|---|---|---|---|---|
| Carnivora | 0 | 0.025 | 12.5 | 0.014 |
| Pholidota | 0 | 0 | 0 | 0 |
| Perissodactyla | **1** | **-0.109** | **100** | **-0.13** |
| Chiroptera | 0 | 0.092 | 0 | 0.062 |
| Cetacea | **1** | **-0.079** | **100** | **-0.123** |
| Artiodactyla | 0 | 0.107 | 0 | 0.042 |
| Soricomorpha | 0 | 0.219 | 34.9 | 0.014 |
| Erinaceomorpha | **1** | **-0.253** | **100** | **-0.308** |
| Primates | 0 | 0.095 | 0 | 0.103 |
| Dermoptera | - | - | - | - |
| Scandentia | - | - | 0 | 0 |
| Rodentia | 0 | 0.006 | **97.4** | **-0.018** |
| Lagomorpha | 0 | 0.101 | 4.6 | 0.034 |
| Proboscidea | **1** | **-0.041** | **74.4** | **-0.02** |
| Sirenia | **1** | **-0.197** | **100** | **-0.225** |
| Hyracoidea | 0 | 0 | 0 | 0 |
| Macroscelidea | 0 | 0 | 0 | 0.197 |
| Afrosoricida | 0 | 0 | 0 | 0.125 |
| Tubulidentata | 0 | 0 | 0 | 0 |
| Pilosa | 0 | 0.386 | **74.2** | **-0.059** |
| Cingulata | 0 | 0.197 | **96.6** | **-0.067** |

The inference of Decline for the 21 orders of Placentalia is shown in Table 4.3. There are 6 orders in decline of diversity considering the BC method, this number increases to 14 orders using the GAP method and drops to 4 orders in the analysis of the perCapita method. Only Cetacea, Perissodactyla, and Sirenia are considered to be in decline of diversity in all the six different treatments. Likewise, the orders Afrosoricida, Chiroptera, and Scandentia were classified as not-decline in all treatments.

**Table 4.3:** Orders in decline of diversity. “1” Decline; “0” not-decline; “-” inconclusive.

| Order | BC | GAP | perCapita |
|---|---|---|---|
| Carnivora | 0 | 1 | - |
| Pholidota | 0 | - | 0 |
| Perissodactyla | 1 | 1 | 1 |
| Chiroptera | 0 | 0 | 0 |
| Cetacea | 1 | 1 | 1 |
| Artiodactyla | - | 1 | 0 |
| Soricomorpha | 0 | 1 | - |
| Erinaceomorpha | - | 1 | 1 |
| Primates | 0 | - | 0 |
| Dermoptera | 0 | - | - |
| Scandentia | 0 | 0 | 0 |
| Rodentia | 0 | - | - |
| Lagomorpha | - | 1 | 0 |
| Proboscidea | 1 | 1 | - |
| Sirenia | 1 | 1 | 1 |
| Hyracoidea | 1 | 1 | 0 |
| Macroscelidea | - | 1 | 0 |
| Afrosoricida | 0 | 0 | 0 |
| Tubulidentata | 1 | 1 | 0 |
| Pilosa | - | 1 | - |
| Cingulata | - | 1 | - |

For the GAP and the perCapita estimates of Decline, it was not possible to distinguish the phylogenetic signal from a randomness nor a brownian threshold scenario, regardless of the phylogenetic hypothesis considered (Table 4.4). The same inconclusive results were found for the analyses with the BC estimate considering the phylogeny of Meredith et al. (2011). Considering the phylogeny of dos Reis et al. (2012), however, it was possible to distinguish the estimated D from the phylogenetic randomness scenario but not from the brownian threshold. This indicates that the Decline model inferred with the BC method is more aggregated than expected by chance in the phylogeny of dos Reis et al. (2012).

**Table 4.4:** Phylogenetic signal for the Decline model for the three different metrics (i.e., BC, GAP, and perCapita rates) and the two different phylogenies (dos Reis et al. 2012 and Meredith et al. 2011) used. Phylogenetic signal was accessed using the D statistic (Fritz and Purvis, 2010). Comparisons are made between empirical D values and the D values expected from a random and Brownian motion models. Significant results are highlighted in bold.

| | dos Reis et al. (2012) | | | Meredith et al. (2011) | | |
|---|---|---|---|---|---|---|
| | BC | GAP | perCapita | BC | GAP | perCapita |
| estimated D | **-3.476** | 2.127 | 0.901 | -1.185 | 1.795 | 1.099 |
| $p(D = D_{random})$ | **0.039** | 0.569 | 0.439 | 0.169 | 0.576 | 0.498 |
| $p(D = D_{BM})$ | 0.889 | 0.319 | 0.423 | 0.698 | 0.321 | 0.379 |

There is no significant phylogenetic signal for the body mass, regardless of the phylogenetic hypothesis considered (Table 4.5), so we used the Point Bi-Serial Correlation to investigate the association with the decline of diversity. We found strong positive correlations between the body mass and the Decline model for all treatments (Figure 4.3). On the other hand, there is no correlation between the body mass and sampling probability ($p = 0.660$; Table IV), which indicates that the association between mass and Decline is not a bias derived from differential preservation. Finally, regardless of the dataset considered, there is no correlation between the footeRates and the body mass ($p_{stg1} = 0.947$, $q_{stg1} = 0.647$, $p_{stg2} = 0.989$, $q_{stg2} = 0.818$; Table II and Appendix V).

**Table 4.5:** Phylogenetic signal for body mass, two measures of disparity, and extinction risk when using two different phylogenies (dos Reis et al. 2012 and Meredith et al. 2011). Phylogenetic signal was accessed using Pagel's $\lambda$ (Pagel, 1999). Significant results are highlighted in bold.

| | dos Reis et al. (2012) | | | | Meredith et al. (2011) | | | |
|---|---|---|---|---|---|---|---|---|
| | mass | MPD | MNND | extRisk | mass | MPD | MNND | extRisk |
| estimated $\lambda$ | 2.141 | 0.000 | 1.948 | 0.000 | 0.000 | **2.617** | **1.909** | 0.000 |
| $p(\lambda = 0)$ | 0.244 | 0.999 | 0.091 | 0.999 | 0.999 | **0.036** | **0.042** | 0.999 |

For the morphological disparity, there was no significant phylogenetic signal in the phylogeny of dos Reis et al. (2012), which indicates that we should use a normal correlation test to assess the association with the Decline model. On the other hand, considering the phylogeny of Meredith et al. (2011) both the MPD and MNND metrics exhibited a significant phylogenetic signal (Table 4.5), which indicates that we should use a comparative method. In order to address this problem, we used both the comparative method GEE, considering Meredith et al.'s phylogeny, and the Point Bi-Serial correlation (see section 3.9). For the GEE method, there was no significant effect of the MNND metric on the decline of diversity ($p_{BC} = 0.855$; $p_{GAP} = 0.594$; $p_{perCapita} = 0.843$). In the analysis of the MPD metric, however, the two characterizations of Decline based on the diversity metrics exhibited a significant negative correlation ($p_{BC} = 0.022$; $p_{GAP} = 0.042$; $p_{perCapita} = 0.241$;

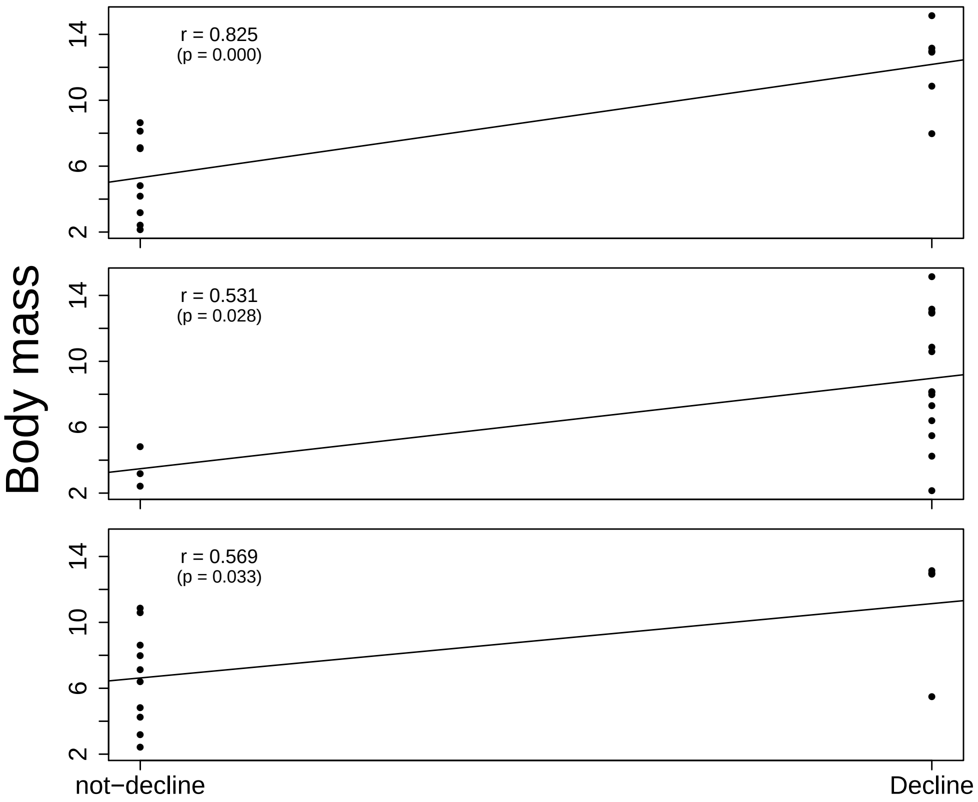

**Figure 4.3:** Correlation between the body mass and the decline of diversity. Top: boundary-crosser estimate. Middle: gap-analysis estimate. Bottom: perCapita rates of diversification estimate.

Figure 4.4). These results are in agreement with the Point Bi-Serial correlation, which indicates a lack of correlation between the decline of diversity and the MNND metric ($p_{BC} = 0.946$; $p_{GAP} = 0.622$; $p_{perCapita} = 0.874$) and a significant negative correlation between the MPD metric and the Decline inferred with the diversity metrics ($p_{BC} = 0.037$; $p_{GAP} = 0.030$; $p_{perCapita} = 0.225$). Finally, there is no correlation between the MPD metric and the footeRates ($p_{stg1} = 0.901$, $q_{stg1} = 0.299$, $p_{stg2} = 0.791$, $q_{stg2} = 0.390$; Appendix V).

There is no phylogenetic signal for the extinction risk (Table III) of the 21 orders of placental mammals (Table 4.5). The Point Bi-Serial Correlation also indicates lack of correlation between the extinction risk and the decline of diversity ($p_{BC} = 0.281$; $p_{GAP} = 0.428$; $p_{perCapita} = 0.147$; Appendix VI).

Lastly, we performed the sensitivity analyzes for the three traits (i.e., body mass, morphological disparity, and extinction risk) by including the orders considered inconclusive (see section 3.4) in the correlation test. There were 6 orders deemed inconclusive with the BC metric, 4 with GAP, and 7 with perCapita (Table 4.3), which wields a total of 64, 16, and 128 comparisons, respectively. The raw values of the correlations for each trait were similar to the ones inferred by excluding the inconclusive orders, with positive correlations between body mass and Decline and negative correlations between MPD and Decline. However, all correlations were considered not significant after applying the Bonferroni correction, which was expected given the high number of comparisons made. The Bonferroni correc-

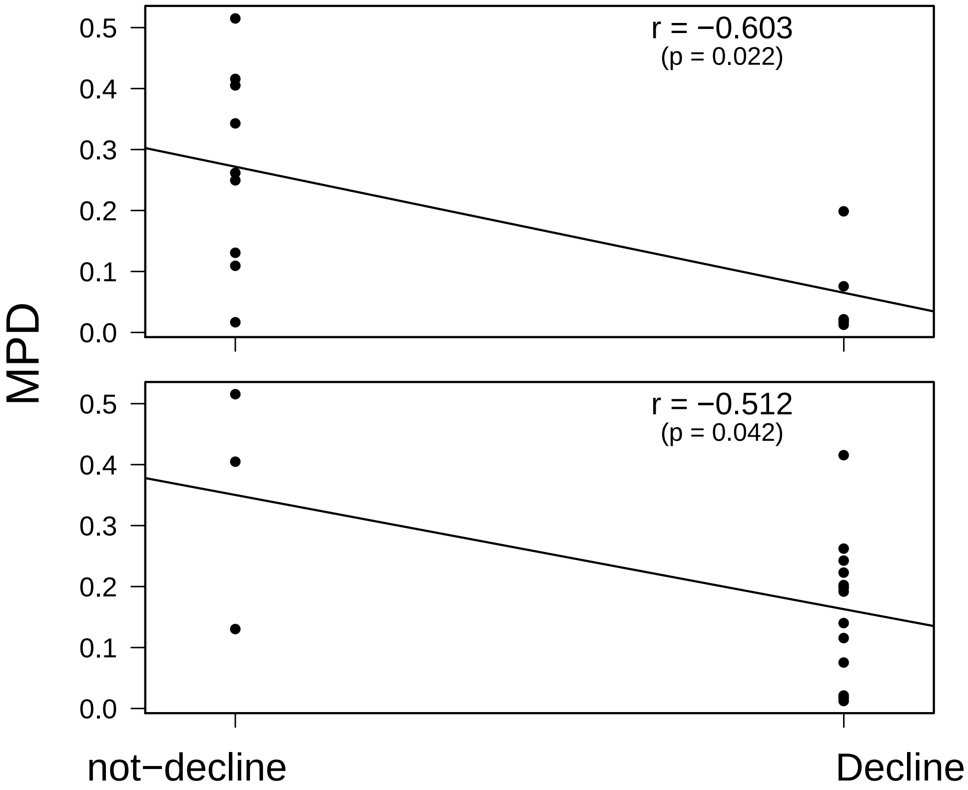

**Figure 4.4:** Correlation between the morphological disparity estimated with the MPD metric and the decline of diversity. Top: boundary-crosser estimate. Bottom: gap-analysis estimate.

tion controls the statistical significance level ($\alpha$) by taking into consideration the number of comparisons made. More specifically, the probability of wrongly inferring a significant correlation between two variables increases with the number of comparisons, hence in order to maintain the same error rate one must correct the $\alpha$. For example, considering a significance level of $\alpha = 0.05$, a p-value of 0.03 would indicate a significant correlation in the case where only one comparison was made. However, if six comparisons were made the significance level with the Bonferroni correction would be $\alpha = 0.05/6 = 0.0083$, and the same p-value of 0.03 would not be considered significant. Therefore, by applying the Bonferroni correction we maintain the same rate of type I error (“false positive”). On the other hand, when a high number of comparisons is made the Bonferroni correction is conservative, once it greatly increases the type II error (“false negative”). We considered those analyses too conservative and based our discussion on the analysis that did not include the orders that could not have its diversity trajectory defined.

# 5 Discussion

## 5.1 Patterns of Decline

Our analysis of the fossil record shows that the majority of the orders of Placentalia present a signal of decline in diversity. The Decline was more pronounced in the analysis with the diversity metrics (i.e., BC and GAP), which indicates that most orders of placentals were more diverse in the deep past. The extant diversity has been thoroughly studied and the number of species described per year has diminished in the last decades (Mora et al., 2011), meaning that most of the diversity has already been described. Hence, the estimate of extant diversity can be interpreted as a perfect fossil record in which almost all the diversity is represented. On the other hand, both BC and GAP were developed to deal with the imperfections of the fossil records, but these metrics can only give a rough estimate of the diversity in the past. So we think our estimates of diversity decline are conservative. The GAP analysis uses the per interval sample probability to correct for the imperfections of the fossil record, but this method does not guarantee the coexistence of the lineages. When the longevity of the lineages is short compared to the duration of the intervals, the GAP most likely overestimate the diversity. The BC is the most restrictive metric and, by estimating the diversity only on the boundaries of the intervals, guarantees that the lineages coexisted in the same time. However, this metric might underestimate the diversity when the average longevity of the lineages is longer than the average duration of the intervals analyzed. In this case there is no need to consider only the lineages at the boundaries, as most of the lineages that occurred within a given interval must have coexisted. In such a scenario the GAP would be a better estimate of the diversity. Looking at our data, the oldest occurrence in the "stg2" dataset is from the Maastrichtian (66.00 - 72.10 Ma), which wields a total of 21 geological stages included in our analyzes. The average duration of these intervals is 3.43 My (Appendix III), which is almost half the estimated genera longevity ("stg1": 5.15 My, "stg2": 6.26 My; Appendix II). Therefore, the BC probably underestimate the number of genera in the fossil record and GAP is the most reliable estimate of diversity for our datasets.

The analysis of Figure 4.2 suggests a relatively stable diversification rate throughout the history of the lineages of Placentalia, which is in line with previous studies (e.g., Bininda-Emonds et al., 2007; Liow and Finarelli, 2014). For the majority of the orders (e.g., Carnivora and Perissodactyla) the rates of diversification were low and varied around zero (Figure 4.2), whereas the rates of extinction and origination varied substantially (Appendix IV). At first sight, such pattern is consistent with an equilibrium dynamics with constant turn-over of lineages (Figure 3.4) and contrasts with the estimated variations of genera diversity (Figure 4.1). However, it is important to note that small diversification rates sustained for relatively long periods of time can have a significant impact on the diversity of a lineage and small rates of diversification, if experienced for relatively longer periods, can produce considerable changes in diversity patterns. Thus, caution should be taken when using the estimated diversification rates to characterize an equilibrium dynamics.

In general, the characterization of Decline was fairly robust to the datasets and it was possible to classify most of the orders. The perCapita method was the least conclusive, with 7 orders considered to be inconclusive. By looking at Table 4.2, it is possible to note that the randomizations of the "stg2" dataset had a significant influence in the determination of decline. In other words, the inference of decline varied depending on how the occurrences were resolved. This is in contrast with the diversity methods. For both BC and GAP, the randomizations had little to no effect on the determination of the diversity trajectory. In general, all the 1,000 randomizations of the "stg2" dataset indicated the same pattern, either Decline or not-decline (Table 4.1). For these metrics the inconclusive category represents inconsistency between the datasets, with the "stg1" usually indicating not-decline. This is specially true for the BC metric in which all 6 inconclusive orders presented different classification depending on the dataset. The robustness of the diversity metrics is probably related to the fact that these methods used the whole trajectory of the orders to characterize the model of diversification. Hence, regardless of the configuration, the occurrences were always counted. In the perCapita method, however, the inference was restricted to the three stages of the Pliocene. Depending on how the occurrences were resolved one might include or exclude a considerable amount of diversification events, which makes the perCapita method more sensitive to the randomizations of "stg2".

There is a discrepancy between the diversity metrics and the perCapita method. The former indicates that the majority of the lineages are in decline of diversity, whereas the latter indicates the opposite scenario with only four orders in Decline and ten orders in not-decline (Table 4.3). One might argue that the discrepancies in the characterization of Decline means that the orders have already recovered from the decline inferred with the diversity metrics. In this case, the Decline model would have been wrongly inferred and the majority of the orders of Placentalia are actually not-decline (Figure 3.4). Here is important to remember that we grouped the Expansion and Saturation models under not-decline (section 3.4), hence the proposed recovery in diversity might have different meanings depending on the subjacent model of diversification. Under an Expansion model there is no significant effect of ecological limits on the diversification trajectory, which is controlled by the dynamic interplay of immigration, extinction, and origination (Harmon and Harrison, 2015). Thus, in an Expansion model the recovery would simply mean the change between a period of loss in diversity to a period of increase in diversity. Under a Saturation model the diversification trajectory of a lineage is controlled by its "carrying capacity", which is a product of the diversity dependence of the rates of origination and/or extinction (Rabosky and Hurlbert, 2015). Hence, in a Saturation model the estimated positive rates would mean that the diversity is currently recovering and is approaching its “carrying capacity”. It is also important to note that the definition of Decline according to the diversity metrics and the perCapita method might mean very different things. In the case of diversity metrics a categorization of Decline means that at some point in the past a given lineage had higher diversity, while definition of Decline based on the Pliocene rates means that in the recent past the lineage experienced negative growth. Therefore, the rates only capture the recent history, while the diversity metrics include the whole history for each lineage. In fact, the Pliocene represents a period of climate oscillations that includes the last warm phase before the formation of continental ice sheets (Janis, 1993, and references therein) and previous studies have assessed the impact of the climate changes during this period on the patterns of diversification (e.g., Fortelius et al., 2006, 2014). In addition, the rates of origination and extinction have different contributions to the decline of diversity (Bambach et al., 2004) and it is common to encounter intervals with increase in diversity even in the waxing phase of a lineage (Quental and Marshall, 2013). Thus, we argue that the characterization of Decline with the diversity and perCapita methods in fact mean different things and we should note that the Pliocene was an unusual geological interval, in which the diversification rates of the declining orders was generally positive.

It is noteworthy that both Cetacea and Sirenia have a strong signal of diversity decline, being possible to detect the Decline even in the raw data (Appendix VII). The same trajectory has been inferred in previous studies (Uhen, 2007; Quental and Marshall, 2010; Morlon et al., 2011) that used different methods and taxonomic unities, showing that the pattern is the same regardless of the methodology and scale analyzed. The orders Cetacea and Sirenia represent independent transitions to the marine realm, each one with unique, although convergent, morphological adaptations (Uhen, 2007). The clear pattern of Decline in these orders indicates that the invasion of the marine habitat, even though allowed for an initial expansion in diversity, might have eventually driven marine mammals into Decline. This conclusion is sustained by additional inspection of the fossil record, as the only other order of marine mammals, Desmostylia, is already extinct (Kemp, 2005, p. 257; see section 5.3 for further details). However, Placentalia is an unusual group with many transitions from land to water, being one of the vertebrate groups with most transitions to aquatic habitat (Vermeij and Dudley, 2000). Hence, this tendency to Decline is in contrast with the apparent propensity of placentals to invade the aquatic environment. In total 24 lineages made the transition to water, of which 7 have also become marine (i.e., Cetacea, Sirenia, Desmostylia, Pinnipedia, polar bear, sea otter, and the extinct aquatic sloths; Uhen, 2007) and the other 17 have remained in fresh water (Vermeij and Dudley, 2000). Given the differences in both environments (Vermeij and Grosberg, 2010), the invasion of the marine realm is associated with several convergent and, usually, sequential adaptations (Kelley and Pyenson, 2015). Thus, the multiple independent invasions of the marine habitat make the marine placentals an excellent model to study the association of traits and the decline of diversity. More specifically, it would be interesting to investigate the possible relationship between the Decline model and the morphological adaptations to the marine habitat. If confirmed that for marine placentals an initial success if followed by a later Decline, this would reinforce the idea that changes in the environment might make a thriving lineage to eventually lose the race to the Red Queen (discussed in section 5.4).

## 5.2 Possible biases

There are mainly three possible biases in our analysis of the fossil record with the diversity metrics. First, one might argue that the classification of the diversity trajectory based on only two points (i.e., the maximum diversity in the fossil record and the extant diversity) is an oversimplification. A clade that is in a dynamic equilibrium with constant turnover of lineages will most likely have some intervals with a spike in diversity. The chance of randomly producing such a peak in diversity will increase the longer the clade stays in the equilibrium, so the orders with the older occurrences would most likely present more points of high diversity. However, if the Decline was only a product of random variation in the diversity, one should expect no consistency along the trajectory of a lineage. The variation of diversity during a dynamic equilibrium should approximate a constrained random-walk, with the peaks in diversity randomly distribute across time. A visual inspection of Figure 4.1 indicates that this is not the case. For the majority of orders considered to be in Decline the intervals with a high diversity are not randomly distributed, instead these intervals appear in sequence. Such a pattern is highly congruent with the expected by the Decline model (Figure 3.4).

Another possible problem with the diversity metrics is the taxonomy. The methods used in the delimitation of genera in the fossil record might be different from the ones used in extant genera, which can result in lumping or over-splitting of the genera (Forey et al., 2004). The former, if practiced by taxonomists of extinct lineages, would introduce a bias against the decline of diversity by reducing the estimated diversity in the past, whereas the latter might lead us to wrongly infer the decline of diversity by overestimating the diversity in the past. A species is assigned to a given genera depending on a complex set of factors, including its genealogical history and the perceived difference from its close relatives (Forey et al., 2004). Given that there is a wealth of data available for the classification of extant genera whereas fossil genera are based only on morphological characters, we argue that it is more likely to split the extant genera than the fossil genera. If this is the case, the actual number of orders in Decline could be higher than what was inferred. Like suggested by Barnosky et al. (2011), probably the best solution would be to re-classify all extant lineages using the same criteria used in the fossil record, but such analysis is not in the scope of this project. An easier way to assess the effect of taxonomy in our results is to compare the relative difference in the absolute numbers of genera. Instead of analyzing when the diversity was higher - either in the past or in the present - we might analyze the magnitude of the difference in diversity. For example, the maximum BC estimated diversity for the order Perissodactyla is 32 genera (“stg1”) and the extant genera diversity is 6 (Table 4.1), which means that the diversity in the past was 5 times higher. So, in order for the differences in the taxonomy to account for this pattern, the taxonomic practice used by the paleontologists would have to split the lineages in the fossil record 5 times more than the taxonomic practices used to define extant lineages. When applying the same logic for the 21 orders, we find that most orders in Decline have an estimated diversity in the past twice as high as the extant diversity (Table 4.1). Such differences are unlikely to have been generated only by taxonomic practices, especially at the genus level; hence we assume that taxonomy had little influence in our results and that our inferences indicate real variations in the diversity of genera.

Finally, we analyzed the diversity dynamics using genera as the taxonomic unity but the pattern at the specific level might be decoupled from the genera diversity (Valentine and Walker, 1986). The Decline was inferred in the cases with more genera in the past, however, it is possible for the number of genera decrease while the number of species remains constant, or even increases, through time. Each genus is composed of closely related species with fairly similar features, so to switch from several species-poor genera to a few species-rich genera would require a dramatic change in the dynamic of diversification of a lineage. Such change in diversification pattern might have occurred for some lineages, but it is highly unlikely for such change to have occurred in more than half of the orders of Placentalia at the same time. In addition, analyzes of different lineages (Sepkoski et al., 1981; Roy et al., 1996; Foote, 2007) demonstrate that the diversification dynamics of the genera is a good indicator of the diversification at the specific level. Moreover, Hadly et al. (2009) proposed that genera might be a better unity of analysis for macroevolutionary studies of niche dynamics in mammals, given that at the generic level it is possible to better characterize the niche of the group and at this level the niche is less labile than at the specific level. In the same line, a recent study (Humphreys and Barraclough, 2014) has shown that the families and genera represent significant evolutionary units in mammals. Thus, we assume that the patterns found in our analyses using genera as taxonomic unity correspond to the dynamics of diversification of species.

The characterization of Decline using the rates in the Pliocene (i.e., perCapita method) is also susceptible to the imperfections of the fossil record described above, but it is harder to predict how the biases would affect the rates estimates. The perCapita rates depend not only on the number of lineages at a given time in point but also on the time of appearance and disappearance of the given lineages in the fossil record (much more than the diversity metrics). An over-splitting of the lineages, for example, might not be enough to produce the patterns of genera diversity encountered with the diversity metrics, but can completely alter the estimates of rates during the Pliocene specially if this over-splitting is not randomly distributed over time (Foote, 2000). It is interesting to note that the taxonomic practices (either over-splitting or lumping) would affect estimates of origination and extinction in opposite ways. For instance, over-splitting lineages might increase origination rate, but it should also increase extinction rates, once there are more species to go extinct. Lumping on the other hand, should decrease origination as well as extinction, reducing the rate of turnover of the lineage. Therefore it is possible that the estimate for each rate might be biased while the estimate of the net diversification rate itself is more accurate.

One way forward to try to circumvent these problems would be to reduce the scope of the analysis, and focus only on lineages that have an extremely good fossil record and then analyze the dynamics of species within families. This analysis would require a lineage that has a good fossil record and with a well established phylogeny. A possible candidate is the order Artiodactyla, which possess almost 20,000 occurrences (Table I) and a fairly complete fossil record (Tables II and IV). In addition, the phylogenetic relationships of the lineages of artiodactyls have been thoroughly studied (Prothero and Foss, 2007), making Artiodactyla a good choice for this analysis. Also, the use of species as taxonomic unit allows one to apply more sophisticated methods, such as capture-mark-recapture models (CMR; Liow and Nichols, 2010) and Silvestro et al.'s (2014) Bayesian approach. The CMR models were developed to estimate recruitment and survivorship for individuals within animal populations, but has been adapted to paleontological data (e.g., Tomiya, 2013; Liow and Finarelli, 2014) to estimate rates of origination and extinction. The Bayesian method developed by Silvestro et al. (2014) can be used not only to estimate the rates of diversification and sampling probability, but also allows one to test for the influence of abiotic and biotic factors on the diversification of the lineages (e.g., Silvestro et al., in press). The use of these methods would allow a better characterization of the diversification dynamics but unfortunately we would not be able to apply them to all placentals given the quality and quantity of the available data for most orders. It would be interesting, though, to apply these more sophisticated methods for the orders with sufficient data, and then compare the results with the conclusions of this study.

## 5.3 Phylogenetic signal

There was no phylogenetic signal for the body mass and the risk of extinction (Table 4.5), which contrasts with previous works (body mass: Smith et al., 2004 and Carotenuto et al., 2010; extinction risk: Fritz and Purvis, 2010) and highlights the importance of testing for phylogenetic signal before applying any comparative method in order to avoid overcorrection (Björklund, 1997). The lack of signal was expected given the hierarchical level analyzed. In both phylogenies the orders have originated more than 50 Ma and have passed most of their evolutionary history (compared to the origin of Placentalia) as separated entities (Figure 3.2). In such scenario it is unlikely to encounter a significant phylogenetic signal. In addition, there are only 21 extant orders of Placentalia and it is hard to detect any signal in the analysis of phylogenies with such small number of tips (Fritz and Purvis, 2010; Nunn, 2011).

The strength of the phylogenetic signal varied depending on the phylogeny (Tables 4.4 and 4.5). This inconsistency highlights the importance of treating the phylogenies as hypotheses and incorporating more than one phylogenetic hypothesis in the analysis. There is a difference of approximately 10 My in the dating of the phylogenies and there are small differences between their topology (section 3.3). However, the small dissimilarities were enough for a complete different result concerning the phylogenetic signal of the morphological disparity and the Decline model. For the disparity there is a significant phylogenetic signal only in the phylogeny of Meredith et al. (2011). Nevertheless, the uncertainty in the estimate of phylogenetic signal had no influence in our results. Both the Point Bi-serial correlation and GEE (section 3.9) indicate a negative association between the MPD and the Decline and lack of correlation for the MNND metric. The congruence between the normal correlation and the phylogenetic comparative metric indicates that the diversification pattern of the morphological disparity did not significantly change throughout the evolution of the lineage (Ricklefs and Starck, 1996). For the Decline model, however, the phylogenetic signal was found in the phylogeny of dos Reis et al. (2012) and only for the BC metric (Table 4.4), which is not as reliable as the GAP estimate (see section 5.1). This apparent lack of signal contrast with the Table 4.3, which shows a nonrandom distribution of Decline among the placental superorders. The superorders Afrotheria and Laurasiatheria appear to be the most affected with the majority of the orders in decline of diversity. In addition, the analysis of both orders of xenarthras is inconclusive, except for the GAP estimate which indicates decline in diversity. Euarchontoglires, on the other hand, was the least affected with only the order Lagomorpha showing Decline (GAP).

Here is important to acknowledge some extinct orders of placentals. The Ptolemaiida is a lineage of wolf-sized afrotheres that lived during the Paleogene (Cote et al., 2007), from the Rupelian to the Burdigalian (33.90 - 15.97 Ma). The origins and even the taxonomic hierarchy of the ptolemaiids are still controversial, with some studies placing them as a subgroup of Soricomorpha (Prothero, 2006, p. 168). The recently extinct order Bibymalagasia was originally considered to be related to Tubulidentata, but recent molecular evidence (Buckley, 2013) suggests that it is related to the family Tenrecidae (Afrosoricidae). The Embrithopoda is another extinct order of Afrotheria (Asher et al., 2003), this rhino-like lineage lived between the late Paleocene until the late Eocene (59.20 - 38 Ma). The Desmostylia (mentioned in section 5.1) is an extinct order of aquatic mammals that existed from the late Oligocene to the late Miocene (28.10 - 7.24 Ma). Traditionally this order is considered a sister-group of Sirenia and Proboscidea (and possibly Embrithopoda) which suggests an aquatic ancestor for the group (Kemp, 2005, p. 257). Nevertheless, a recent analysis (Cooper et al., 2014) places Desmostylia as a stem group of Perissodactyla, indicating that its morphological similarities to Sirenia and Proboscidea is a case of morphological convergence. Also, the order Afredentata is based on the ant-eating genus *Eurotamandua* which inhabited Europe during the Eocene (56.00 - 33.90 Ma). Afredentata is traditionally considered an extinct order of Xenarthra (Gaudin and Branham, 1998), however, Rose (1999) argues that the morphological features used to classify this group represent a case of convergent evolution and Afredentata is a sister-group of Pholidota. The extinct order Creodonta lived from the Paleocene to the Miocene (65.50 - 5.33 Ma) and is considered to be a sister-group of Carnivora (Bajpai et al., 2009). In addition, Dinocerata is an order of Laurasiatheria (Lucas, 1993) that includes the largest herbivores from the Paleocene until the Eocene (65.50 - 33.90 Ma). Finally, Meridiungulata represents an extinct superorder of South American placental mammals, composed by five orders: Pyrotheria, Xenungulata, Litopterna, Notoungulate, and Astrapotheria (McKenna, 1975). Some controversies concerning the monophyly as well as the origin of this superorder still remain (Kemp, 2005, p. 242).

Given the lack of data for these fossil lineages as well as the uncertainty regarding their taxonomy, we were unable to include them in our analyzes. Nevertheless, it is possible to note that the extinction pattern is highly asymmetric. The superorders Afrotheria and Laurasiatheria were the most affected. These superorders comprehends at least seven of the extinct lineages mentioned above. If we consider that most extant orders of Afrotheria and at least half the orders of Laurasiatheria already present an indication of diversity decline (Table 4.3), it is possible to predict that the inclusion of these lineages in the phylogeny would change the phylogenetic signal of the Decline model.

## 5.4 The effect of traits on diversity decline

Our correlation analysis indicated a positive association between the average body mass and the Decline of the orders. This positive correlation was highly consistent, being found with the three metrics used to characterize the diversity trajectory (Figure 4.3). It is also interesting to note that all the extinct orders of placentals (see section 5.3) were composed of large animals (i.e., more than 10kg), which is consistent with the hypothesis that larger body size makes a lineage more prone to Decline. Such association might seem, at first glance, to be unexpected and temporally unstable given that a trait with a negative effect on the diversification should either lead the lineage to go fully extinct and therefore the association should disappear (macroevolutionary response), or lead selection to prune out those traits (microevolutionary response). Thus, the fact that some large lineages of placental still persist might suggest: 1- that the potential advantage of large body size existed only at a the determined geological point in the past and at a certain time there was a change in the selective pressures that turned larger body size into a disadvantage, but not enough time has passed for large lineages to become fully extinct; 2- that selection for body size might have opposite directions at different hierarchical levels (individual vs species) and therefore larger body size recurrently emerges through individual selective pressure to later cause a macroevolutionary disadvantage; 3- that larger placentals have a diversification dynamics that is more prone to stochastic fluctuations and therefore suffer stronger variations that would more easily produce a pattern of decline diversity compared to small placentals (discussed in the next section). Those possibilities do not exhaust all possible scenarios and the reality might be more complex than such depiction, but those represent promising starting points on trying to explain the pattern recovered here. It should also be noted that it is inherently difficult to directly test mechanistic hypothesis with historical data but investigating the potential correlation between body size and diversification dynamics, how the evolution of body size might affect the pattern of morphospace occupation, and how ubiquitous and recurrent among placental mammals is the trend to increase body size (i.e., Cope's rule) might help us understand how plausible those mechanisms are.

Cope's rule was first proposed based on data from the fossil record and a variety of studies have assessed its prevalence in mammals. One of the best-known examples of Cope's rule is Alroy's (1998) analysis of North America mammalian fossil record. In this study, Alroy investigated mammals as whole and assumed an ancestor-descendant relationship without a proper phylogenetic analysis. He found an average of 9.1% increase in body mass for the large mammals. However, this study is geographically restricted and the dynamic of body size evolution in North America may be different from other regions. In addition, there are several problems with assuming a direct ancestor-descendant relation given the incompleteness of the fossil record (Foote, 1996). A posterior analysis, using an expanded version of the dataset compiled by Alroy (1998), concluded that there is no compelling or consistent support for any trend in the body size evolution of North American mammals (Lovegrove and Mowoe, 2013). Although some lineages present a short-time pattern of increase in body size, Lovegrove and Mowoe (2013) conclude that Cope's rule fail to apply to all mammalian lineages within any geological period of time analyzed. On the other hand, Raia et al. (2012) constructed a phylogeny of large fossil mammals and encountered a 10-fold increase in the mean mammal body size during the Cenozoic (65.5 Ma - recent). In principle, this study encompasses mammals of the whole World, but there is a bias for the orders Perissodactyla and Artiodactyla of North America and Eurasia. More problematic, Raia et al. (2012)'s analysis is restricted to large mammals only. Lastly, although the use of an explicit phylogenetic hypotheses by Raia et al. (2012) is clearly an improvement over previous analyses, the method is similar to the one used by Alroy (1998) and thus has similar limitations pointed out by Foote (1996).

Although it has been pointed out that it is extremely difficult to investigate macroevolutionary trends using solely extant species (Monroe and Bokma, 2010; Quental and Marshall, 2010; Slater et al., 2012; Finarelli and Goswami, 2013) the study of Baker et al. (2015) found evidence for Cope's rule without the use of fossil data. These authors applied Venditti et al. (2011)'s method to estimate changes in the rate of morphological evolution in mammals, and found a positive correlation between the body mass and rate of morphological evolution. In addition, the same authors estimated the ancestral body sizes at the nodes of the phylogeny, using different parameters for each order, and encountered that descendant species are on average 6% larger than their ancestors. Moreover Baker et al. (2015) suggested, based on the analysis of the relationship between ancestral state estimate and the tendency for increase in size, that Cope's rule in mammals is an active trend. As with the fossil record, there are a limitations associated with studies using molecular phylogenies and extant species to estimate evolutionary morphological trends (Monroe and Bokma, 2010; Slater et al., 2012; Finarelli and Goswami, 2013). Of particular interest here is the argument presented by Solow and Wang (2008) who pointed out that body size may be measured in different ways which influences the detectability of the trend, being possible to find evidence either for or against the trend in the same lineage depending on the metric used. Hence, these authors advise caution when interpreting the evidence in favor and against Cope's rule. Also, recent studies (Novack-Gottshall and Lanier, 2008; Hopkins and Smith, 2015) highlight the importance of considering the scale used in the analysis, given that the processes of body size evolution may vary among the different taxonomic levels and geological times analyzed (but see Rego et al., 2012).

Therefore the ubiquity of Cope's rule for mammals as whole, either through the lens of the fossil record or molecular phylogenies, has been challenged. On the other hand, the evidence of Cope's rule for some specific lineages of mammals seems less controversial. Slater et al. (2012) developed a novel Bayesian approach that combines fossil evidence with a molecular phylogeny and allows the comparison among several models of trait evolution. This approach was used to study the body size evolution in Carnivora and Slater et al. (2012) found a pattern consistent with Cope's rule. Additionally, Finarelli and Goswami (2013) found evidence of Cope's rule in Canidae, a family of Carnivora. All of the best 10 (out of 300) models of trait evolution considered pointed to a trend towards larger size (Finarelli and Goswami, 2013). Moreover, the analyzes of the evolution of horses (MacFadden, 1994; Shoemaker and Clauset, 2014), sloths (Pant et al., 2014), and pinnipeds (Churchill et al., 2015) indicate an increase of body size through time. While the first studies with horses - an iconic Cope's rule example - were based mostly on fossil data, the last two studies constructed a phylogeny that includes extinct and extant species, although used different methods to analyze the patterns of size evolution. Pant et al. (2014) used a modified version of the models developed by Hunt (2007). Whereas Churchill et al. (2015) reconstructed the body size for the nodes of the phylogeny and analyzed the changes along the branches (similar to Butler and Goswami, 2008). All those studies support Cope's rule for specific lineages, however, the mode as well as the magnitude of body size evolution varied considerably depending on the taxonomic level and geological time considered. We therefore suspect that Cope's rule is not a universal phenomenon across all mammals but rather a phenomenon specific to some lineages. The fact that different mammalian lineages with different times of origin have shown independent changes in the evolution of body size (Venditti et al., 2011) and that our analysis suggests that the lineages entered decline in different points in time (see Figure 4.1), indicate that the potential advantage of large body and its supposed disadvantage probably did not have a defined synchronic temporal schedule for all mammals but rather suggests an episodically emergence through the history of Placentalia that is independently experienced by some, not all lineages. It is still an open question if such trend is the product of varying selective regimes experienced by each lineage or stochastic variation on diversification dynamics across different lineages.

In accordance with a scenario of a shifting regime on selective pressures, Shoemaker and Clauset (2014) proposed that changes in body size on horses are related to climate changes. Although this suggests a change in environment that might have acted as a selective regime to explain why lineages became progressively bigger it does not necessarily explain why such increase in size would eventually lead to the decline of diversity we see on Equidae (Quental and Marshall, 2013). The work of Van Valkenburgh et al. (2004) on the other hand, suggested that increases in body size on two extinct sub-families of Canidae (presumably due to individual advantages of being larger), predisposed those animals to evolve hyper-carnivory. These authors then showed that such dietary habit made larger hyper-carnivorous animals more likely to go extinct. Therefore this later study clearly advocates that selection at individual level might eventually result on a higher level cost (Jablonski, 2008b), a scenario that has been described by some authors as “evolutionary suicide” (Rankin and López-Sepulcre, 2005). In fact the study of Goldberg et al. (2010) on species selection provides another clear example of such higher level costs. Goldberg et al. (2010) investigated the evolutionary dynamics of reproductive strategies in the plant family Solanaceae (Asterids). The plants of this family present either self-incompatibility (SI; i.e., the ability of individual plants to recognize and reject their own pollen) or self-compatibility (SC). The former (SI), is thought to be the plesiomorphic state and transition from SI to SC is an extremely common evolutionary shifts, whereas the opposite shift (from SC to SI) seems to have never occurred in Solanaceae (Goldberg et al., 2010). More interestingly, this study found that extinction rates associated with self-compatibility exceed the speciation rate associated with the same reproductive mode. Therefore the evolution of SC (presumably through individual level selection) leads to negative diversification rates, and the only reason we still see this trait is because it recurrently re-evolve from an self-incompatible ancestral. These examples highlight the possibility that natural selection might act on different levels of evolutionary hierarchy and suggest that an “evolutionary suicide” might be possible. We advocate that the patterns recovered in our analysis are in accordance with such scenario of conflicting selection at different levels of organization. It is clearly impossible to explicitly test such hypothesis with historical data, but the plausibility of such scenario on explaining our results should rest on the validity of some of its logical assumptions and proposed mechanisms. First there should be evidence that individuals with bigger size have higher fitness, second that such selection regime could eventually generate the deep time trend in increase body size (Cope’s rule), and lastly that the evolution of bigger body size could eventually lead to either increased extinction or decreased speciation.

There are some examples in mammals that suggest that bigger individuals have higher fitness (Trivers, 1972; Festa-Bianchet et al., 1998). On the other hand evidence for Cope’s rule in microevolutionary studies is a bit more controversial. In 2004, Kingsolver and Pfennig compiled a large database of studies that estimated phenotypic selection in the field. The traits measured in each study were assigned to "body size" or "other morphological traits" and the latter was subdivided into three categories according to how the traits affected the fitness (i.e., survival, fecundity, mating success). In all cases the "other morphological traits" and its subcategories showed no bias in any direction. On the other hand, the distribution of selective pressure on the "body size" was strongly skewed towards positive values, which Kingsolver and Pfennig (2004) interpreted as evidence for Cope's rule. Nevertheless, in a recent study Gotanda et al. (2015) found no evidence of increase in size in extant organisms. The authors compiled a dataset with more than 1,000 records of recent (i.e., in the last hundred years) morphological change and divided the traits in the same categories as Kingsolver and Pfennig (2004). Surprisingly, there was no trend towards large body size in their dataset. Gotanda et al. (2015) attribute the contradictory results to the fact that most estimates of selective pressure are low and that other evolutionary forces may be operating (e.g., covariance between nonheritable traits and fitness). However, it should be noted that those studies encompasses many different taxa, not only mammals, and that there might be some heterogeneity in the tendency to evolve larger body size. Therefore the incongruent evidence might be more related to the fact that not all lineages will present Cope's rule than to the fact that selection at a shorter time scale will not result in such a trend.

Interestingly one of the few empirical examples of conflict of selection at different hierarchical levels involves body size (Muir and Howard, 1999). In this case, the authors inserted the human growth hormone gene into a small cyprinodont fish (*Oryzias latipes*), then conducted several experiments to document different aspects of the fitness. The transgenic fish had bigger body size and were preferred by females, but presented lower fecundity (Muir and Howard, 1999). Based on the empirical observations Muir and Howard (1999) predicted that the release of transgenic fish would eventually lead to the extinction of such species. Clearly this is not a natural situation, but it demonstrates that body size might be advantageous at the individual level while making the species more prone to go extinct. Other potential costs have been associated with large body size. For example, for mammals there seems to be a positive association between body size and risk of extinction (Cardillo et al., 2005). On the other hand Silvestro et al. (in press) have found no direct effect of body size per se on the changes in speciation or extinction rates. It is therefore possible that the increase in body size might indirectly affect the probability of decline. In fact it has been shown that body size is correlated with other traits that are more directly associated with extinction risk (e.g., population density; Cardillo et al., 2005) and, as mentioned above, that evolution of body size indirectly affects extinction by favoring hyper-carnivory in Canidae (Van Valkenburgh et al., 2004). Looking at other aspect of body size evolution might shed some light into the likelihood of macroevolutionary costs on lineages that evolved large body size.

Along those lines, our results suggest that one of the measures of morphological disparity (mean pairwise distance - MPD) is negatively correlated with Decline (Figure 4.4). MPD is a measure of the body size variation within each order, hence the negative association indicates that orders in Decline have less morphological variation. The low variability could be interpreted either as the cause or as a consequence of the Decline. In the first scenario, the inability of the order to generate morphological diversity could ultimately lead the lineage to perish. One potential argument would rest on the idea that lineages with low morphological disparity represent lineages that have some kind of constraint that might eventually impose a higher cost when faced with constantly changing environment (Van Valkenburgh, 1999; Moen and Morlon, 2014). So under this hypothetical scenario a limited array of possible morphological options might eventually lead to a decrease in speciation and/or a rise in extinction for lineages that eventually took that evolutionary path. Indeed decline in diversity for mammal lineages seem to be related to changes in both speciation and extinction rates (Quental and Marshall, 2013). There are several possibilities why the dynamics of a given lineage might change, and those ideas come from the pioneering work of (Van Valen, 1973) which suggests a zero-sum game with a constantly deteriorating environment (the Red Queen hypothesis). Ever since, several macroevolutionary studies have examined this theory, specially trying to determine whether the selective pressure comes from abiotic or biotic factors (e.g., Benton, 2009; Ezard et al., 2011a; Voje et al., 2015). Of particular interest is the possibility of clade competition (Van Valkenburgh, 1999). It is possible that active clade competition experienced by lineages with lower disparity (or larger body size) is particularly higher, especially if such competition comes from multiple clades. In fact the evolution of hyper-carnivory (Van Valkenburgh, 1999; Van Valkenburgh et al., 2004) mentioned above could be viewed as an example of an evolutionary cost associated with lower morphological disparity. Throughout the evolutionary history of mammals, different taxonomic groups evolved towards hyper-canivory (i.e., larger than 7 kg and diet composed of at least 50% vertebrates), occupying the large predator adaptive zone. The hyper-canivores were replaced by other hyper-canivore lineages that were previously absent or at low diversity, forming the so called double-wedge pattern in which the waning of one clade is followed by the waxing of a second clade. In total, Van Valkenburgh (1999) identified seven potential examples of double-wedge, with competition being suggested to be the main driver of the replacement in at least three cases. In the other four cases competition played a passive role, suppressing the invasion of the hyper-carnivory niche before the incumbent lineage went extinct. According to Van Valkenburgh (1999) some hyper-carnivore lineages would be morphologically highly specialized, morphologically constraint, and hence potentially unable to adapt to fast changing environment pressures making them more likely to decline. This hypothesis is line with the “cause” scenario proposed above, in which the placental orders studied here with large body size also show low variability in the morphospace and which could therefor translate into their inability to respond to selective pressures and potentially be driven to extinction. Under this scenario it is possible that the evolution of large body size eventually leads to lower morphological variation, therefore rendering an indirect effect to Cope's rule on the macroevolutionary cost (Raia et al., 2012). An alternative view would be that the lineages with higher morphological constraints would go extinct simply by chance (from a macroevolutionary perspective). Under this scenario inability to generate different morphologies would lead to a smaller number of lineages, which in turn could make a lineage more prone to Decline by chance (similar to the effect of population size in Population Genetics). There are some evidences pointing towards a correlation between the morphology and diversity of a lineage (e.g., Gardezi and da Silva, 1999; McClain and Boyer, 2009; Rabosky et al., 2013), however, the correlation is not necessary. For the proposed dynamics to take place, there only needs to exist a limit for the number of lineages that can coexist with the same morphology.

On the other hand, it is possible that the low variability we see on orders that are experiencing decline would in fact be a consequence of Decline, not a cause. Under this scenario the lineages that experienced decrease in diversity or that were not able to diversify in number of species in the past would experience a recent reduction in their morphological disparity (also called "Contraction model" by Bush and Novack-Gottshall, 2012). Such scenario is expected when a lineage is experiencing extinction selectivity (Foote, 1997), in which some traits are preferentially pruned (e.g., Lyons et al., 2004; Jablonski, 2005, 2008a). Several previous studies have focused on the study of extinction selectivity (reviewed in McKinney, 1997), specially in the context of the current diversity crisis (e.g., Purvis et al., 2000). Nevertheless, it is noteworthy that a trait being correlated with higher extinction probability (i.e., extinction selectivity) does not necessarily means the same trait makes a lineage more prone to Decline. The decline in diversity is the product of both the rates of extinction and origination, and these rates might play different roles in the diversity decrease (Bambach et al., 2004). Thus, there might be a positive association between a trait and extinction risk but no association between the same trait and the decline in diversity, in case the origination rate is also higher.

One way to try to differentiate the "cause" and "consequence" scenarios would be to include morphological data from the fossil record in the analysis and investigate how the morphology of the extinct lineages is distributed in relation to the extant lineages of the 21 orders of Placentalia. If the morphology of fossil lineages were basically the same, this would indicate that the lineages were not able to morphologically diversify, in line with the "cause" scenario. On the other hand, if the extinct lineages occupied a different region of the morphospace, then this would indicate some kind of extinction selectivity as predicted by the "consequence" scenario. Unfortunately such analysis is currently difficult given the quality of the fossil record. Another approach to differentiate the scenarios would be to fit different models of trait evolution (e.g., Slater et al., 2012) to the clades in Decline. For the "cause" scenario, a model with a certain degree of constraint (e.g., Ornstein-Uhlenbeck model; Diniz-Filho, 2000) would be the best fit. For the "consequence" scenario, however, a model with changes in the evolutionary dynamics (e.g., accelerating/decelerating evolution model; Slater et al., 2012) would be the best fit.

When taking together our results, and the evidences on the literature regarding different aspects of body size evolution and its potential effects at the individual and lineage level, we suspect that the evolution of body size, driven by individual level selection, eventually created a macroevolutionary cost at the lineages level and drive those different Placentalia orders with substantially large body size to diversity decline. It is also tempting to propose that such increase in body size would lead to more constraint occupation of the morphospace but that remains an open question.

## 5.5 The effect of traits on diversification rates

Clearly the decline of diversity is controlled by changes in speciation and extinction, and there is some evidence that those changes have a deterministic component (e.g., Quental and Marshall, 2013). However, it is possible that an association between average body size and Decline, discussed in the previous section, results from a very specific relationship between body size and diversification dynamics where the demise of clades with large individuals could be the result of a purely stochastic process. If larger animals also have larger speciation rate and larger extinction rate, but still a positive albeit small net diversification rate, it is possible that such scenario could lead to a diversity dynamics more prone to stochastic fluctuations and therefore diversity decline. Under this scenario lineages with large body size would have very high speciation and extinction rates. Given that higher speciation rates might lead to explosive radiations, and that higher extinction rates could eventually more likely remove species this mechanism could, in theory, generate a burst followed by a decline.

Some studies have in fact investigated the effect of the body size on the rates of diversification. Liow et al. (2008) found evidence of higher origination and extinction rates for larger mammals, indicating a more dynamic diversification pattern. Similarly, a recent study done by Tomiya (2013) also found higher extinction rates associated with animals with large body size for both North American and western Eurasian Miocene land mammals. Although the result is consistent with Liow et al. (2008), Tomiya (2013) argued “size selectivity hinges on the biogeographic and environmental contexts of faunal evolution”. The degree of size-biased extinction varied not only between continents but also through time and the extinction of small and large mammals were tightly correlated more often than not. Tomiya (2013) attributes the higher extinction probability of larger mammals to the moments of higher environmental instability, so it is possible that such correlation is simply a by product of “being at the right place at the right time”. It is important to note that both studies divided the lineages into large and small, which is an oversimplification of the body size distribution of the lineages (Figure 3.5). More troublesome, given that it was not possible to directly estimate the size of many placentals, the lineages were assigned to either large or small depending on their taxonomy. This approach with only two size categories, whereas understandable given the imperfections of the fossil record, probably miss a lot of the variation in diversification rates and may incorrectly estimate the effect of body size on the rates, hence the results of Liow et al. (2008) and Tomiya (2013) should be viewed with caution.

Although such stochastic scenario could in theory explain the relationship between decline and body size seen in our study, the results found by Quental and Marshall (2013) suggest that such mechanism is very unlikely. Mammal lineages suffering diversity decline (or fully extinct) clearly switch their dynamics at some point, speciation drops and extinction rises (Quental and Marshall, 2013) so a depiction simply based on an average rate, as done by Liow et al. (2008) and Tomiya (2013), might be misleading and should be interpreted with caution. Additionally, mammal lineages on decline or fully extinct lived for a shorter amount of time than would be expected by change (Quental and Marshall, 2013), which further suggests a deterministic mechanism. We should note, however, that Quental and Marshall (2013) evaluated the behavior of mammals as a whole so it is an open question if such general mammals behavior does not hind specific dynamics associated with lineages of large and small animals.

Although we made the extreme simplification of looking at the average rate of diversification, we looked at the potential relationship between rates and either body size or morphological disparity. We found no association between estimated per-capita rates of origination or extinction (i.e., footeRates) and the two traits (body size and morphological disparity) analyzed. Therefore we do not find evidence that body size affects rates of origination or extinction in a simple manner, as proposed by Liow et al. (2008) and Tomiya (2013). These results also raise the question of how the body size and the morphological disparity might in fact affect the diversification dynamics of the orders of Placentalia. Our simpler, perhaps naïve, expectation was that clades on decline would show either lower average origination and/or higher average extinction rate, given that these traits have shown to be significantly correlated with the Decline (Figures 4.3 and 4.4). One possibility is that the relationship between the trait and the footeRates are more complex, with the traits affecting different rates (i.e., origination or extinction) depending on the context. For instance, higher extinction rates associated with larger body size seems to be common within Neotropical species (Fritz et al., 2009). Also it might be possible for some lineages to respond differently to changes in the body size, with bigger size affecting only origination or solely extinction. For example, a bigger body size, which is usually related to a better vagility, might affect or not the rate of origination depending on the geography of a region. In a region where a bigger lineage has less barriers to dispersal, hence it is more difficult to isolate populations, there might be a drop in the origination rate. In another region the increase in size might not change the dispersal rate (e.g., an island), but the lower population density, usually associated with larger lineages, might increase the extinction rate. In fact context-dependence of the rates of diversification has been shown in the studies of the impact of different trophic level on diversification (Price et al., 2012), as well as, the relationship between latitude and rates (Rolland et al., 2014).

Another possibility to explain the lack of correlation between traits and the footeRates is a methodological limitation related to the use of average rates. In our analysis all the 21 orders of Placentalia have extant species, hence the net diversification rate for all of them is positive, even for the orders with a clear decrease in diversity (e.g., Cetacea and Perissodactyla). By estimating the footeRates as the weighted mean for the whole range of each order, it is not possible to in fact differentiate a declining lineage from a not-decline lineage, even if the trait has predictable effect on both the origination and extinction rates. One way to circumvent this problem would be to focus only on the orders in Decline, using an approach similar to Quental and Marshall (2013). In this study the authors used the point of maximum diversity in order to differentiate the “waning” phase (i.e., all stages prior to the point) from the “waxing” phase (i.e., all subsequent stages), and investigated the role of each rate in the different phases. For our case, we should find a significant correlation between the average rates in the “waxing” phase and the values of the traits analyzed here.

## 5.6 Diversity decline and risk of extinction

The correlation analysis indicates that the extinction risk of extant species is not associated with the diversity decline inferred from the fossil record. Such lack of correlation might suggest that the drivers of the current and the past Decline are not the same. The current diversity crisis is highly selective, preferentially pruning specific parts of the tree of life (McKinney, 1997). A study by Purvis et al. (2000), for example, indicates that in the scenario where all threatened mammal species went extinct there would be a total loss of about 50% more genera than the expected by chance, which shows that the extinction is nonrandom. Furthermore, the extinction of all threatened mammal species would scale up to hierarchical levels above the genus, and could lead to extinction of several species-poor families and even whole orders (Purvis et al., 2000). The high selectivity indicates that the threatened lineages might share some intrinsic traits that make them more vulnerable to extinction. The relationships between the traits of a lineage and the risk of extinction have been thoroughly explored, with several traits showing extinction selectivity (McKinney, 1997; Cardillo et al., 2005), however, larger body size appears to be preferentially pruned (Cardillo et al., 2005), once it correlates with several traits under selection. Moreover, larger mammals are not only at greater risk, but are also subject to more threat types than smaller mammals Gonzalez-Suarez and Revilla (2014), which lead some authors to explore the possible implications of the disappearance of the large mammals (Dirzo et al., 2014). It is therefore curious that we do not find any correlation between extinction risk and decline (Appendix VI) given that decline was associated with body mass (Figure 4.3). We suspect this lack of association is in fact a product of past extinctions. The same pattern of extinction selectivity, with larger body sizes being preferentially pruned, was found in the Pleistocene megafauna extinction, in which human activities also played a major role (Lyons et al., 2004). Therefore it is possible that some lineages in Decline (this study) might have already lost most of their species while the remaining species could be viewed as extinction “resistant”. Under this scenario we would expect to find several lineages in Decline with lower fraction of genera under risk, while those that are still on the process of loosing most of its diversity would still show a considerable fraction of genera at risk. In fact if we look at the data (Appendix VI) we see that the lineages in not-decline show a considerable smaller variance on extinction risk than lineages in Decline, as well as, current extinction risk that are never as high as the ones found for lineages in Decline. So it is indeed possible that the higher variance in extinction risk seen for orders in Decline result from some of those orders having already lost most of its diversity. This highlights the complexity of these relationships, with the same trait responding differently depending on the hierarchical level analyzed and time scale considered (Levin, 1992; Jablonski, 2007).

# 6 Conclusion

Traits have a great impact on the diversification dynamics of a lineage either by interacting with the abiotic environment (e.g., Collar et al., 2011) or by controlling the intra- (e.g., Brown and Maurer, 1986) and interspecific (e.g., Wagner and Estabrook, 2014) interactions. The majority of studies on diversification dynamics has considered traits in the context of adaptive radiations, in which traits would confer selective advantages and allow for a radiation, such as viviparity in vipers (Viperidae; Lynch, 2009) and nectar spurs in angiosperms (Rieseberg and Willis, 2007, and references therein). However, the possible negative effects of traits on the diversification of a lineage have barely been investigated. The few studies to address this possibility (Van Valkenburgh, 1999; Van Valkenburgh et al., 2004; Goldberg et al., 2010, this study) suggest a complex evolutionary dynamics with several selective pressures acting in different time scales and hierarchical levels. The given trait would confer a selective advantage in one level or time scale, but would be pruned out in another. Under this scenario, a given trait is expected to appear and disappear multiple times throughout the evolutionary history of a lineage, being generally associated with the decline in diversity. This complex scenario appears to be the case for the hyper-carnivory in mammals (Van Valkenburgh, 1999; Van Valkenburgh et al., 2004) and the self-compatibility in Solanaceae (Goldberg et al., 2010). The present study also suggests that larger body size in Placentalia might negatively affect the diversification dynamics, as predicted by previous works that analyzed the dynamics of body size evolution (Hone and Benton, 2005; Clauset and Erwin, 2008). We note that our results are phenomenological in nature and further studies (see sections 5.4 and 5.5) are needed in other to elucidate the processes responsible for the complex evolutionary dynamics of body size and diversity in placentals. Nonetheless, we found that diversity decline is not aggregated through the history of Placentalia, and that lineages that evolved large body size were more likely to enter a phase of diversity decline.

Moreover, by also analyzing the occupation of the body morphospace we proposed two distinct scenarios related to the demise of a given lineage. We found a negative correlation between the Decline model and the disparity metric (Mean Pairwise Distance) that indicates the variation in the occupancy of the morphospace. This result suggests that clades in Decline are more clumped in the morphospace than clades in not-decline. To explain such empirical pattern we proposed two scenario, one where the low morphological variation would be the cause and another where it would be the consequence of diversity decline. Future studies could differentiate between these scenarios and investigate whether the reduced morphological variation of declining lineages is also detected in a multivariate analysis of the morphospace.

Finally, the apparent decoupling of the deep time decline in diversity (this study) and the current diversity crisis (Barnosky et al., 2011; Dirzo et al., 2014) highlights the importance of considering the scale in the study of patterns of evolution (Levin, 1992; Jablonski, 2007). Further studies are needed in order to illuminate both fields, as understanding the drivers of the Decline in the fossil record is required to better comprehend the consequences of the current diversity decline.

# Resumo

O efeito de caracteres intrínsecos na dinâmica de diversificação foram extensamente investigados e diversos caracteres foram associados com aumentos na diversificação. Contudo, os possíveis efeitos negativos de um caractere sobre a diversificação de uma linhagem foram em grande parte ignorados. No presente trabalho integramos o registro fóssil com dados moleculares para estudar a dinâmica de diversificação de Placentalia, focando nas ordens em declínio de diversidade, e investigamos possíveis mecanismos responsáveis por gerar os padrões de diversificação encontrados. Mais especificamente nós: 1- determinamos quais das 21 ordens de Placentalia estão em declínio de diversidade (i.e., Declínio); 2- investigamos se o Declínio apresenta um sinal filogenético; 3- testamos a hipótese de que o tamanho do corpo está relacionado com o Declínio; 4- testamos a hipótese de que as ordens em Declínio possum menor disparidade morfológica; 5- investigamos se as ordens em Declínio, inferido a partir do registro fóssil, são as mesas com maior risco de extinção na atualidade. Nossas análises indicam que a maioria das ordens de mamíferos placentários apresentam um signal consistente com o Declínio e, embora o Declínio não esteja igualmente distribuído entre as superorderns de Placentalia, não há um signal filogenético significativo para as ordens em Declínio. Nossos resultados indicam uma correlação positiva entre o Declínio e o tamanho corporal médio de cada ordem que está de acordo com estudos prévios sobre evolução do tamanho do corpo. Argumentamos que estes resultados sugerem uma dinâmica de evolução complexa: tamanho corpóreo grande seria um atrator evolutivo que gera a tendência das linhagens aumentarem de tamanho, todavia, o aumento do tamanho do corpo seria contrabalançado pela maior susceptibilidade ao Declínio. Outrossim, encontramos uma correlação negativa entre o Declínio e a variação morfológica. Argumentamos que essa correlação poderia indicar dois possíveis cenários: (i) a baixa variação morfológica seria responsável pela redução no número de linhagens e tornaria as ordens mais susceptíveis ao declínio de diversidade; (ii) a baixa variação morfológica teria sido gerada pela diminuição da diversidade. Por último, o risco de extinção das espçeies atuais não está correlacionado com o Declínio, o que sugere que os mecanismos responsáveis pelo Declínio no passado e no presente não são os mesmos.

**Palavras-chave: Placentalia, Macroevolução, Tamanho do corpo**

# Abstract

The effects of intrinsic traits on the diversification dynamics have been extensively investigated, with several traits being associated with increase in diversification. On the other hand, the possible negative effects of traits on the diversification of a lineage have been for the most part overlooked. Here we used both the fossil record and molecular data to study the diversification dynamics of Placentalia, focusing on the orders in decline of diversity, and investigated different mechanisms that might control the evolutionary success of the 21 placental orders. More specifically we: 1- determined which of the 21 orders of Placentalia are in decline of diversity (i.e., Decline model); 2- investigated whether the Decline model has a phylogenetic signal; 3- tested the hypothesis that the differences in body size are related to the Decline model; 4- tested the hypothesis that the orders in Decline have lower morphological disparity; 5- investigated whether the orders in decline of diversity, inferred from the fossil record, are the ones with higher extinction risk nowadays. Our analysis indicate that the majority of the orders of placental mammals have a pattern consistent with the Decline model and, although the Decline model is not equally distributed among the placental superorders, there was no significant phylogenetic signal for the orders in diversity decline. We found a positive correlation between the Decline model and the average body size which is in line with previous studies on body size evolution. We argue that such results suggest a complex evolutionary dynamics: larger body size appears to be an evolutionary attractor with lineages showing a tendency to increase in size, however, the increase in body size would be counterbalanced by a higher propensity to Decline. Moreover, we found a the negative correlation between the Decline model and morphological variation. We suggest that such results could indicate two possible scenario: (i) the low morphological variation would cause lineages to loose diversity; (ii) the low morphological variation would be the product of decrease in diversity through extinction selectivity. Finally, we found no correlation between the extinction risk of extant species and the deep time diversity decline, which suggests that the drivers of the current and the past Decline are not the same.

**Keywords: Placentalia, Macroevolution, Body size**

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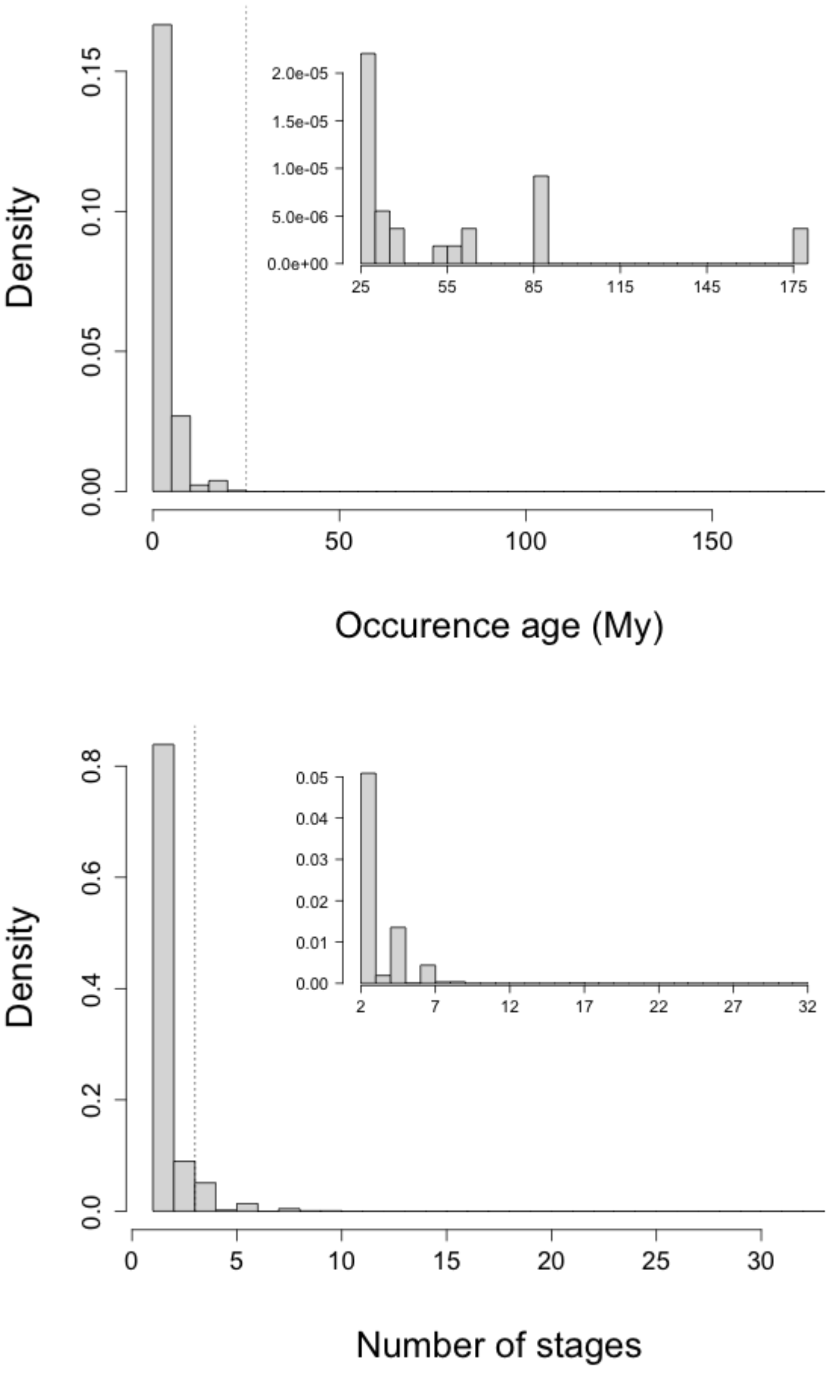
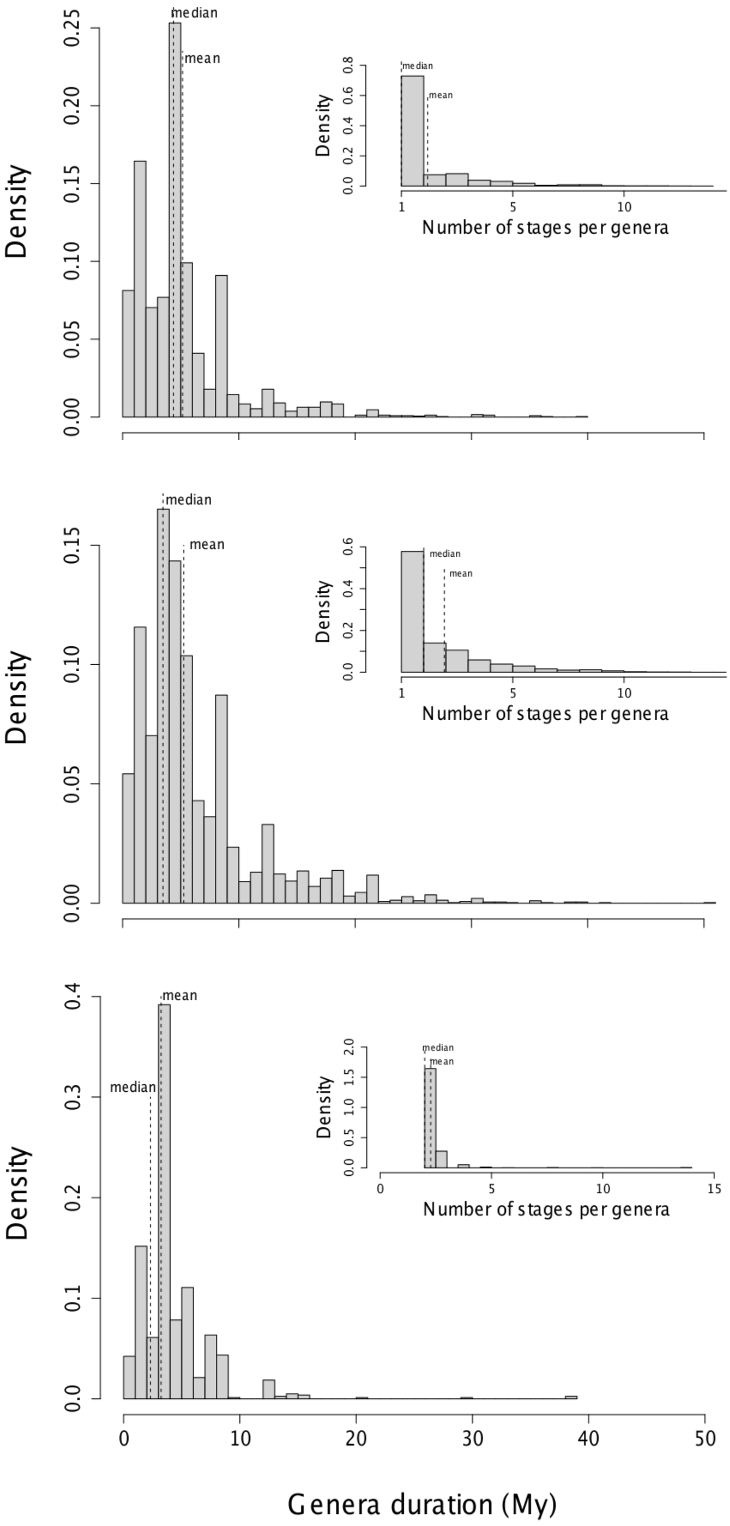
# Appendix

**Table I:** Number of fossil occurrences and genera in the fossil record for the 21 orders of Placentalia.

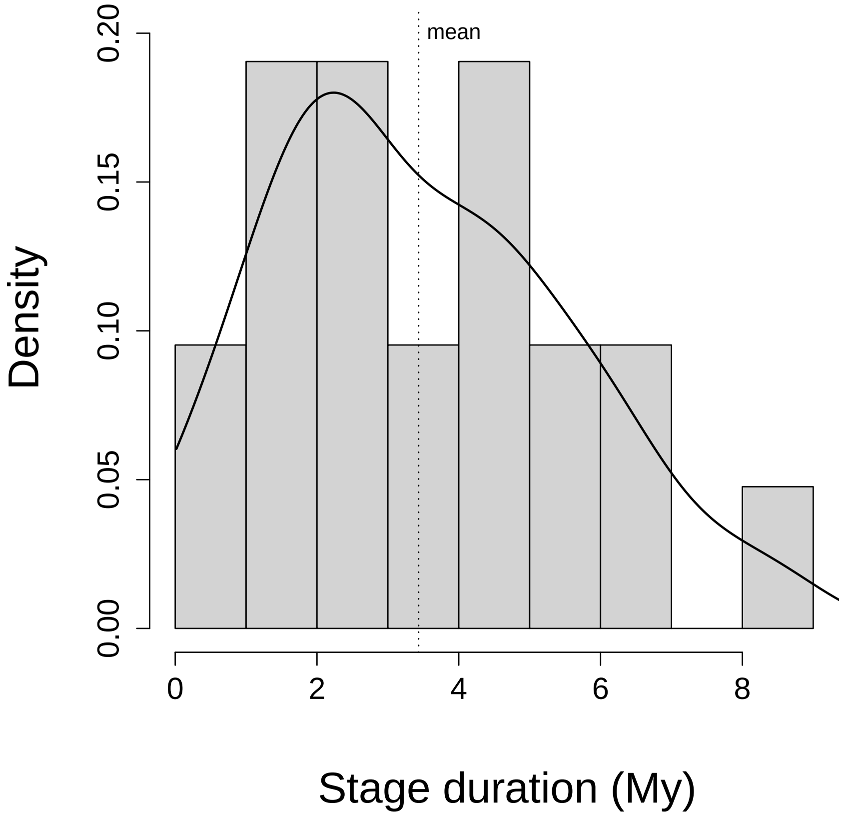
| Order | stg1.Occ | stg2.Occ | stg1.Genera | stg2.Genera |
|---|---|---|---|---|
| Carnivora | 7578 | 1710 | 456 | 565 |
| Pholidota | 16 | 14 | 3 | 6 |
| Perissodactyla | 6422 | 897 | 225 | 288 |
| Chiroptera | 830 | 330 | 109 | 136 |
| Cetacea | 2130 | 848 | 351 | 384 |
| Artiodactyla | 11724 | 2158 | 552 | 701 |
| Soricomorpha | 970 | 283 | 81 | 101 |
| Erinaceomorpha | 233 | 135 | 41 | 52 |
| Primates | 2726 | 636 | 264 | 331 |
| Dermoptera | 31 | 7 | 3 | 5 |
| Scandentia | 5 | 8 | 4 | 4 |
| Rodentia | 14491 | 3072 | 807 | 1009 |
| Lagomorpha | 1703 | 280 | 58 | 73 |
| Proboscidea | 2316 | 323 | 50 | 64 |
| Sirenia | 391 | 127 | 41 | 48 |
| Hyracoidea | 156 | 82 | 24 | 28 |
| Macroscelidea | 562 | 84 | 28 | 42 |
| Afrosoricida | 49 | 17 | 12 | 13 |
| Tubulidentata | 80 | 24 | 3 | 3 |
| Pilosa | 323 | 119 | 37 | 72 |
| Cingulata | 351 | 161 | 50 | 78 |



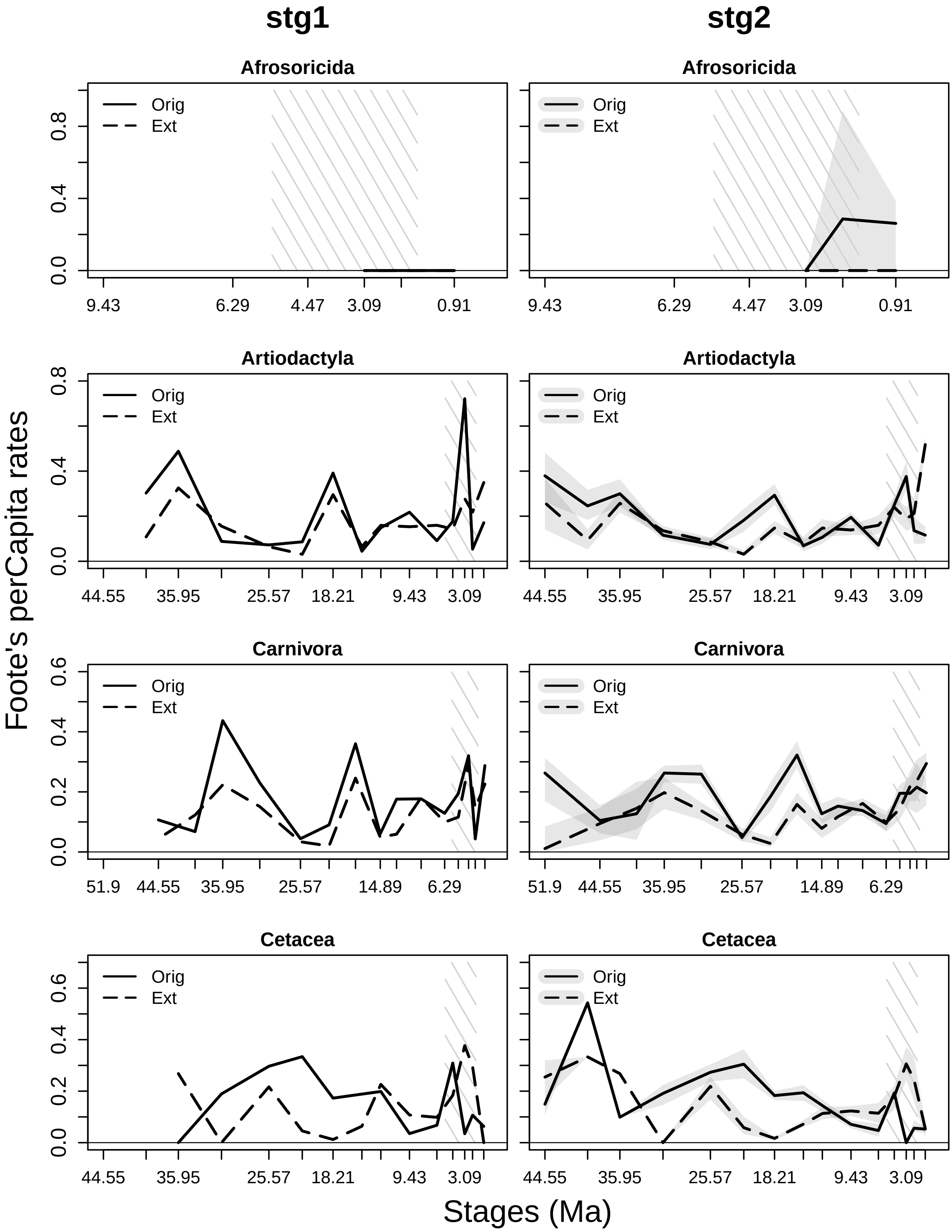
**Appendix I:** Distribution of occurrences durations. Top: duration in Million years; highlighted: distribution of durations for occurrences that encompasses more than 25 My. Bottom: duration in number of stages; highlighted: distribution of number of stages for the occurrences that encompasses more than two stages.



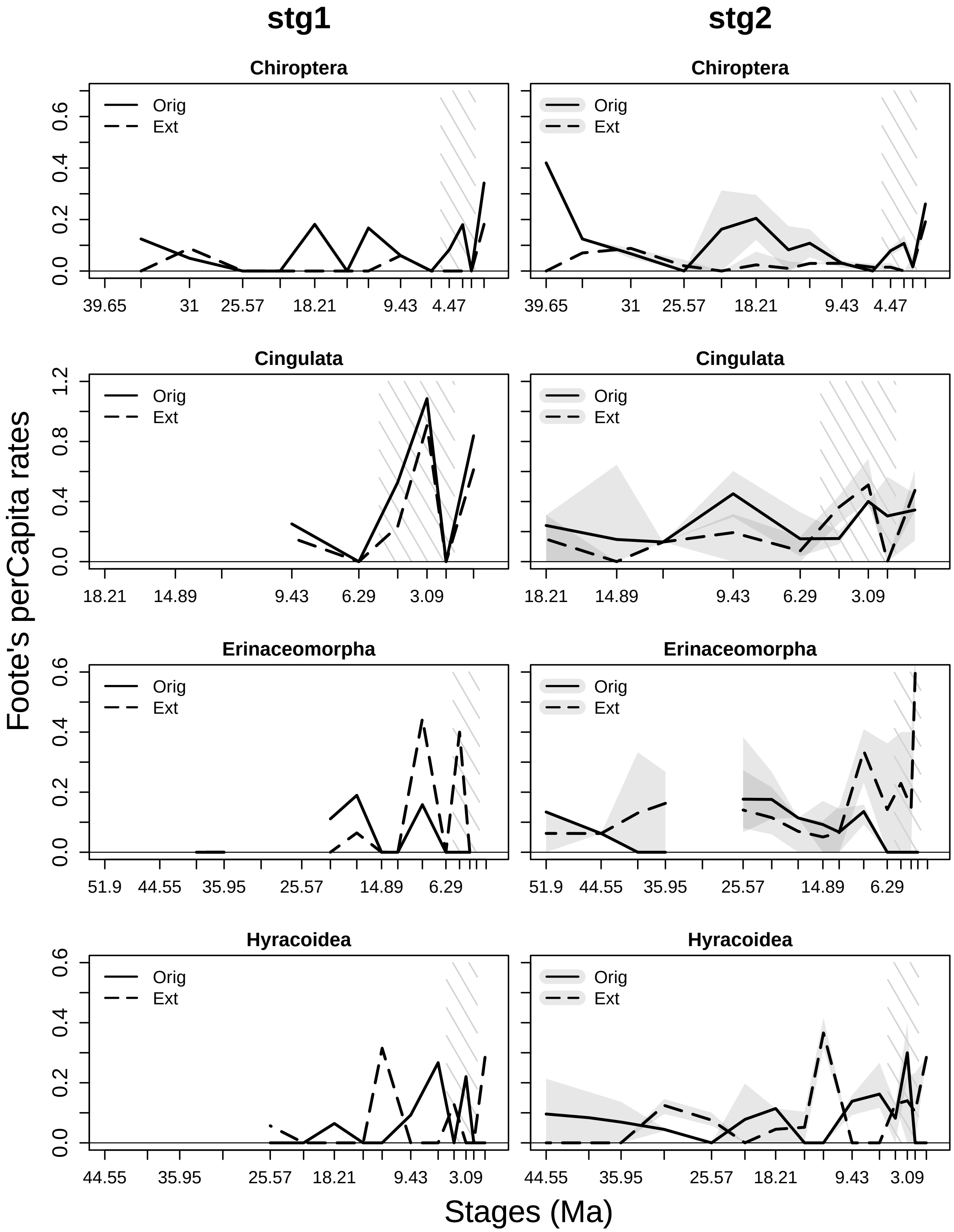
**Appendix II:** Distribution of genera duration. Top: distribution for the "stg1" dataset; Highlighted: distribution of the number of stages per genera. Middle: distribution for the dataset with occurrences limited to 2 stages; Highlighted: distribution of the number of stages per genera. Bottom: distribution of the 804 genera that only appear in the dataset with occurrences limited to 2 stages; Highlighted: distribution of the number of stages per genera.



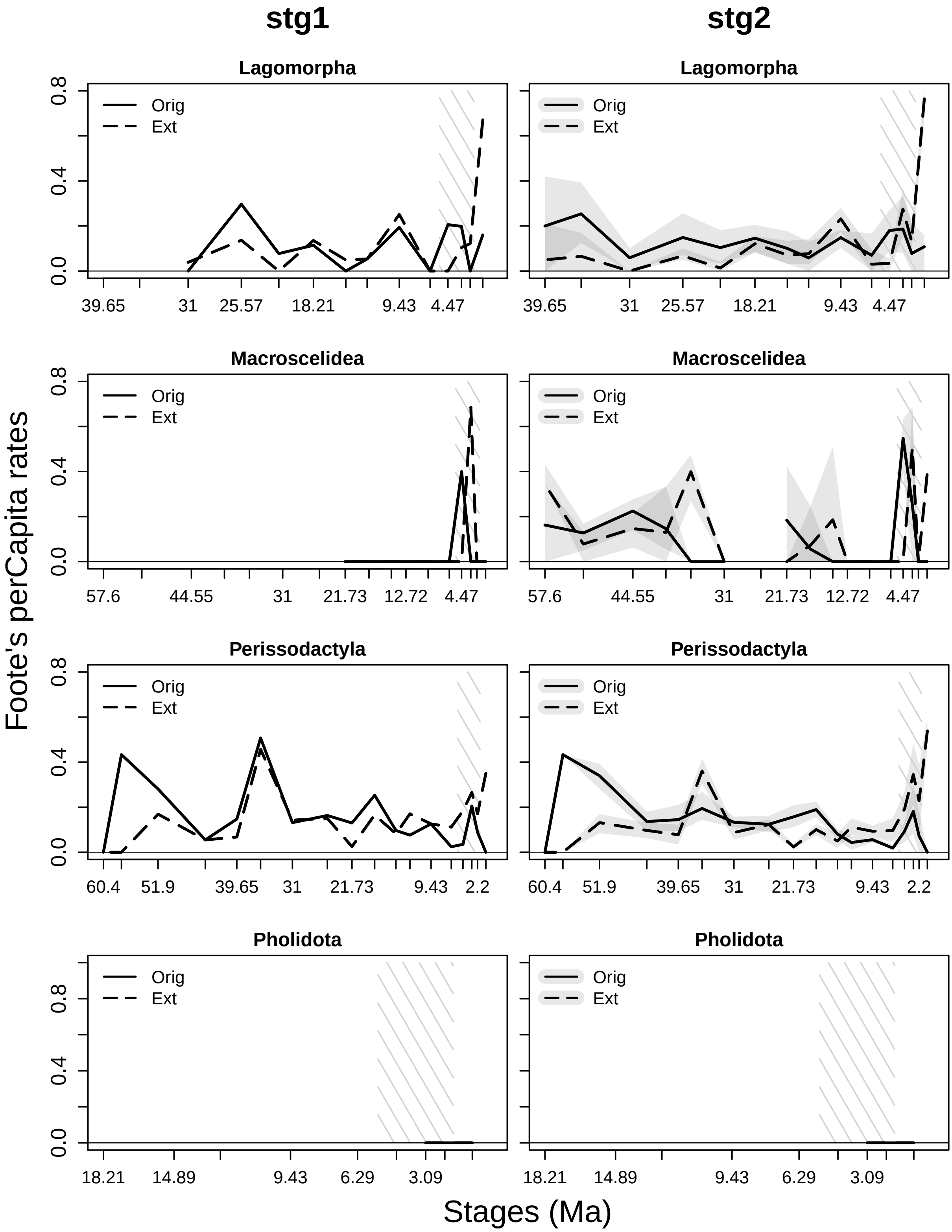
**Appendix III:** Distribution of durations for the 21 most recent geological stages, from the Holocene (0.000 - 0.0117 Ma) to the Maastrichtian (66.0000 - 72.1000 Ma). Solid line: the adjusted density curve. Dotted line: the mean of 3.43 My.



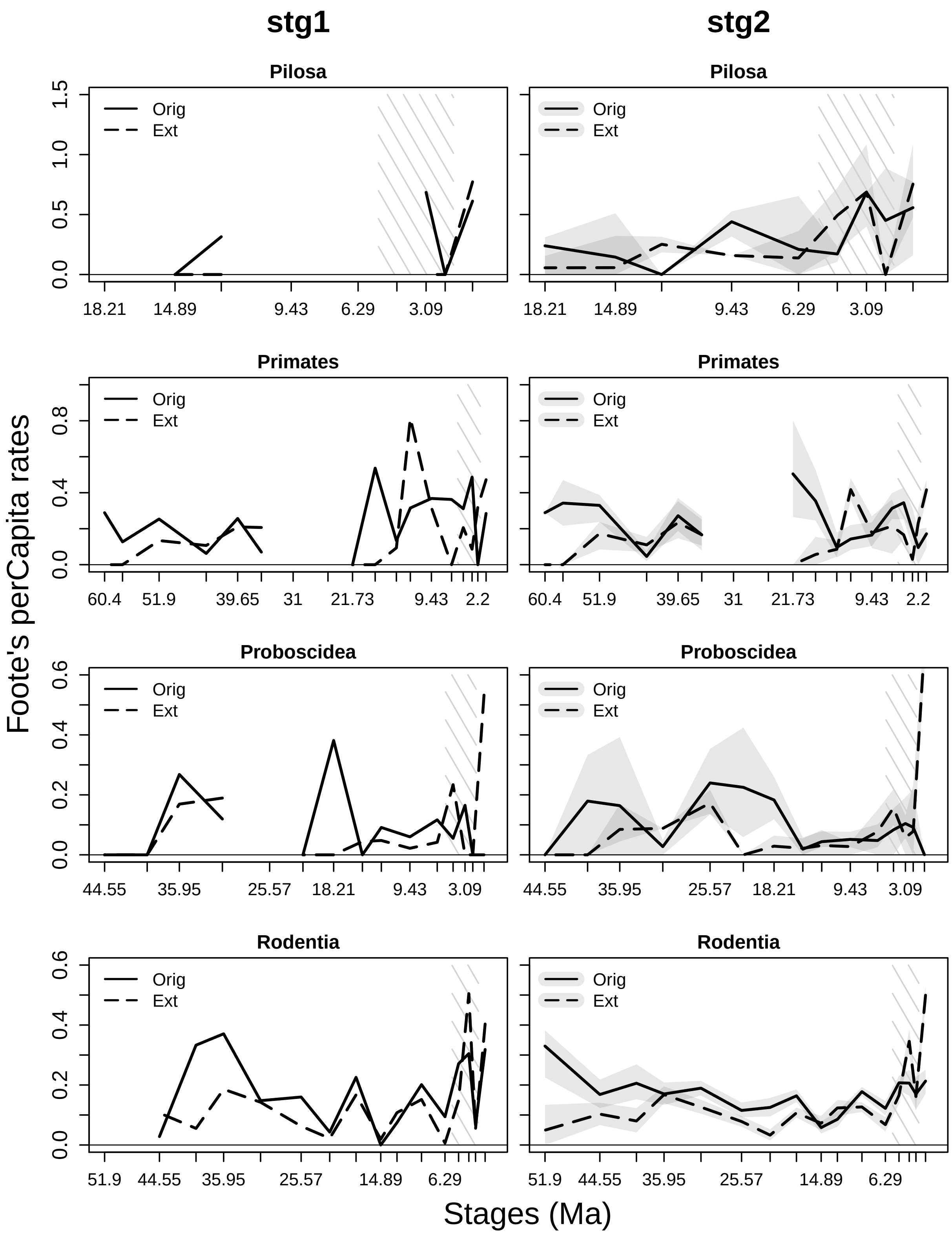
**Appendix IV:** Rate of origination and extinction for the 21 orders of Placentalia. Left: estimates based on "stg1". Right: estimates based on the 1,000 randomizations of "stg2"; the grey area contains 95% of the estimates. The shaded area represents the Pliocene (5.332 - 1.806 Ma). Note: the order Dermoptera do not have any rate estimate.



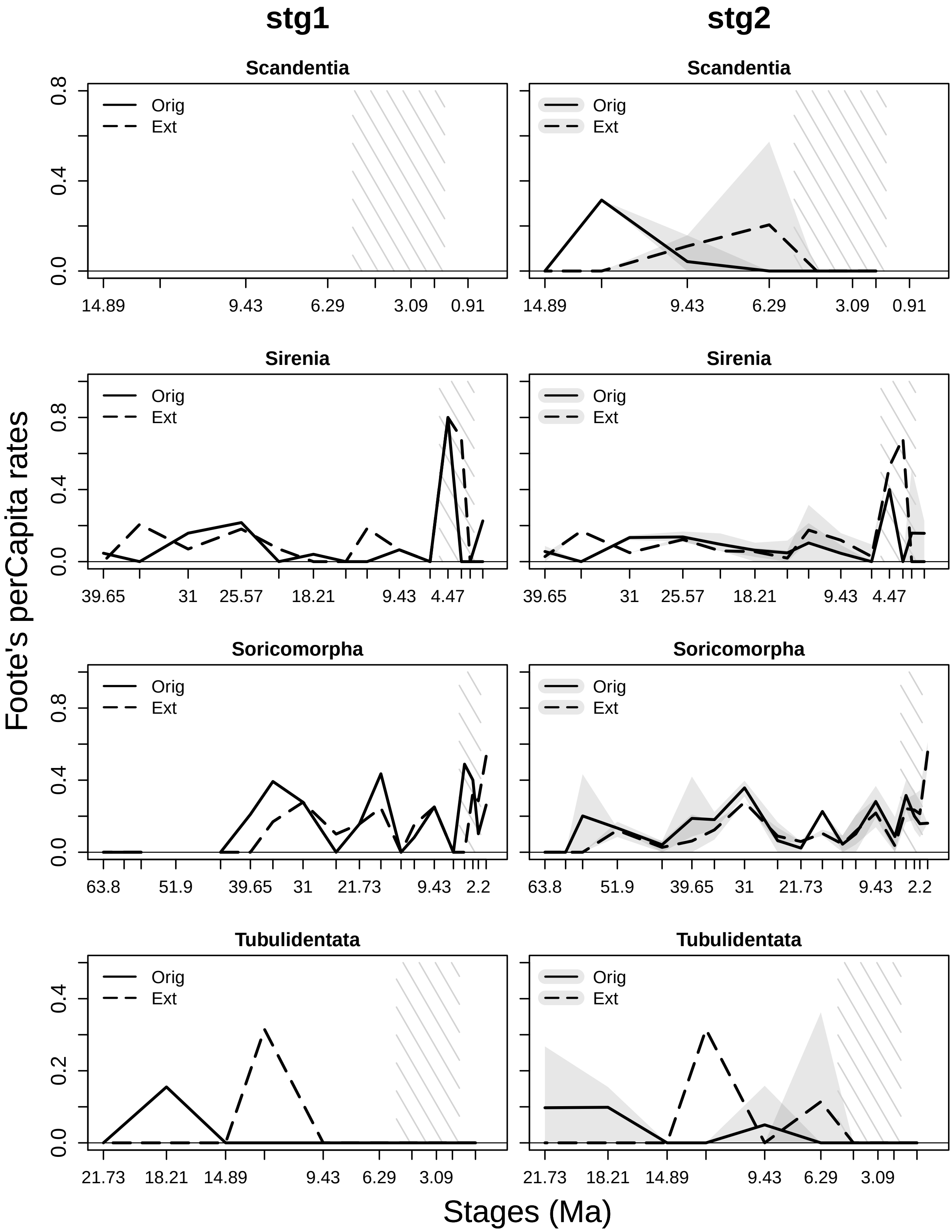
Appendix IV cont.



Appendix IV cont.



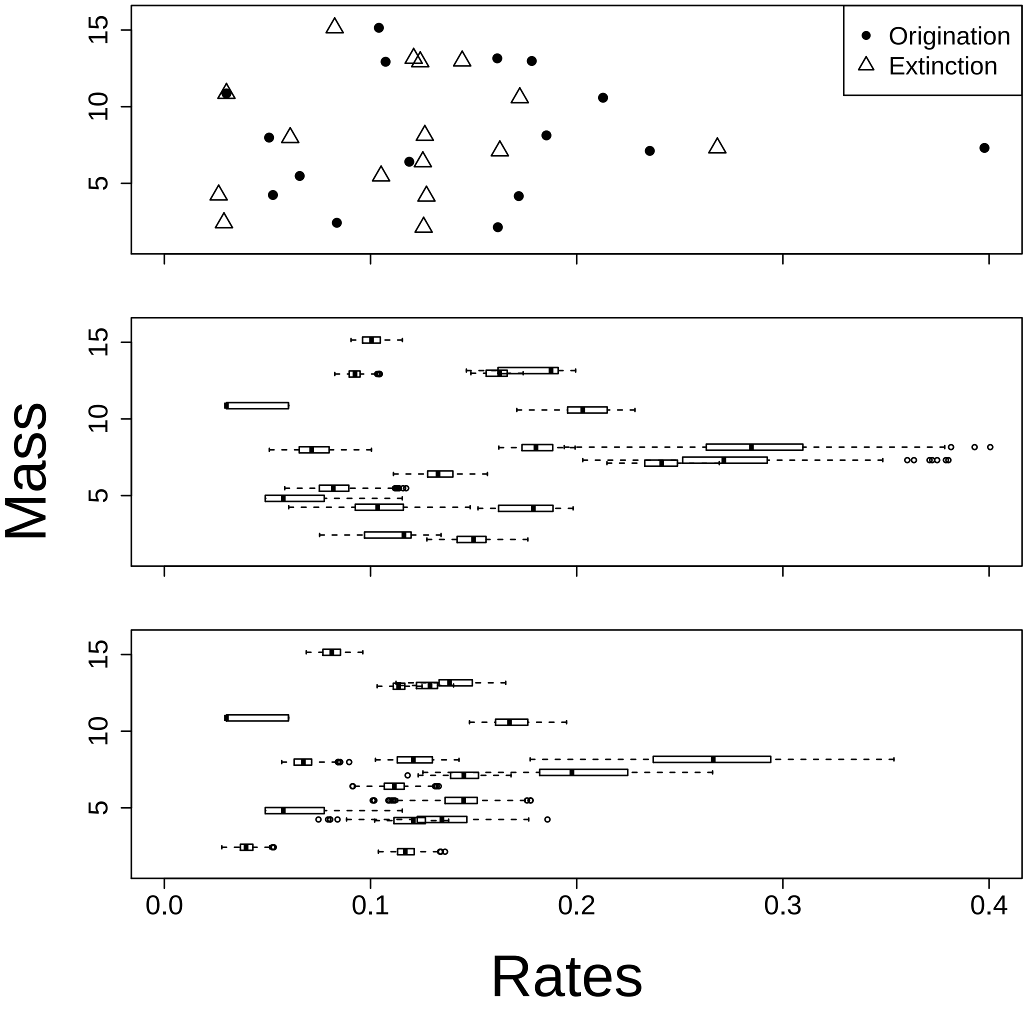
Appendix IV cont.



Appendix IV cont.

**Table II:** Estimates of origination and extinction rates for the whole range of each order of Placentalia. “stg1”: estimates for the “stg1” dataset. “stg2”: estimates for the 1,000 randomizations of “stg2”. “orig” and “ext”, respectively, the origination and extinction footeRates. “perc”: percentage of stages for which it was possible to estimate the footeRates. Note: the orders Afrosoricida, Dermoptera, and Pholidota have rates estimates for less than half of their ranges and were excluded from the analysis.

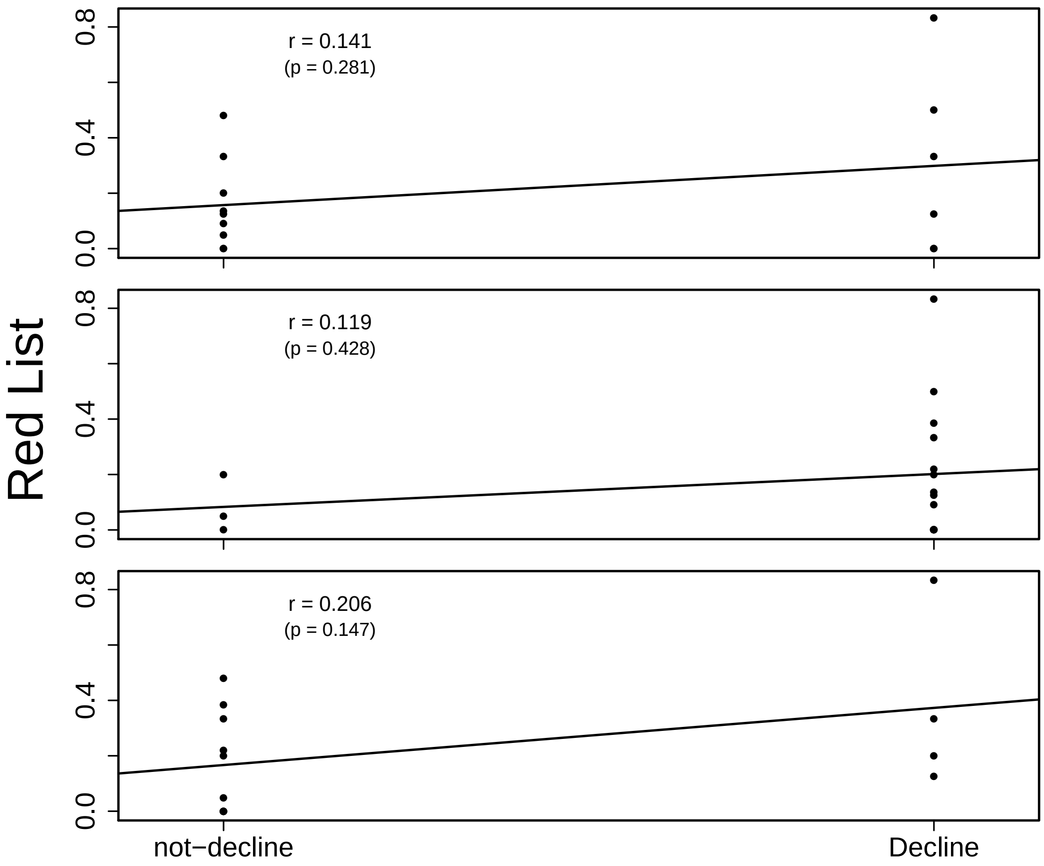
| | stg1 | | | stg2 | | | | |
|---|---|---|---|---|---|---|---|---|
| Order | orig | ext | perc | orig | ext | perc | mass | MPD |
| Carnivora | 0.19 | 0.13 | 78.95 | 0.18 | 0.12 | 81.77 | 8.13 | 0.26 |
| Perissodactyla | 0.18 | 0.14 | 94.74 | 0.16 | 0.13 | 94.74 | 12.98 | 0.08 |
| Chiroptera | 0.08 | 0.03 | 81.25 | 0.11 | 0.04 | 84.94 | 2.43 | 0.52 |
| Cetacea | 0.16 | 0.12 | 81.25 | 0.18 | 0.14 | 88.86 | 13.15 | 0.20 |
| Artiodactyla | 0.21 | 0.17 | 87.50 | 0.20 | 0.17 | 93.24 | 10.58 | 0.14 |
| Soricomorpha | 0.16 | 0.13 | 90.00 | 0.15 | 0.12 | 90.59 | 2.14 | 0.42 |
| Erinaceomorpha | 0.07 | 0.11 | 71.43 | 0.08 | 0.14 | 84.09 | 5.48 | 0.19 |
| Primates | 0.24 | 0.16 | 84.21 | 0.24 | 0.15 | 84.21 | 7.12 | 0.25 |
| Scandentia | - | - | - | 0.06 | 0.06 | 55.80 | 4.82 | 0.13 |
| Rodentia | 0.17 | 0.13 | 93.75 | 0.18 | 0.12 | 92.66 | 4.17 | 0.34 |
| Lagomorpha | 0.12 | 0.13 | 92.31 | 0.13 | 0.11 | 92.63 | 6.41 | 0.22 |
| Proboscidea | 0.10 | 0.08 | 82.35 | 0.10 | 0.08 | 88.24 | 15.15 | 0.02 |
| Sirenia | 0.11 | 0.12 | 87.50 | 0.09 | 0.11 | 87.50 | 12.93 | 0.02 |
| Hyracoidea | 0.05 | 0.06 | 68.75 | 0.07 | 0.07 | 93.46 | 7.98 | 0.01 |
| Macroscelidea | 0.05 | 0.03 | 57.89 | 0.10 | 0.13 | 76.42 | 4.24 | 0.24 |
| Tubulidentata | 0.03 | 0.03 | 90.91 | 0.04 | 0.04 | 90.91 | 10.87 | - |
| Pilosa | - | - | - | 0.29 | 0.26 | 51.19 | 8.16 | 0.12 |
| Cingulata | 0.40 | 0.27 | 66.67 | 0.27 | 0.20 | 84.37 | 7.31 | 0.20 |



**Appendix V:** Rates of origination and extinction for the whole range of the orders as a function of body mass. Top: origination and extinction rate estimates based on the "stg1" dataset. Middle and Bottom represent, respectively, the origination and extinction rate estimates based on the 1,000 randomizations of "stg2"; the boxplot represent a summary of the estimates for each order.

**Table III:** Percentage of genera in risk of extinction for the 21 orders of Placentalia.

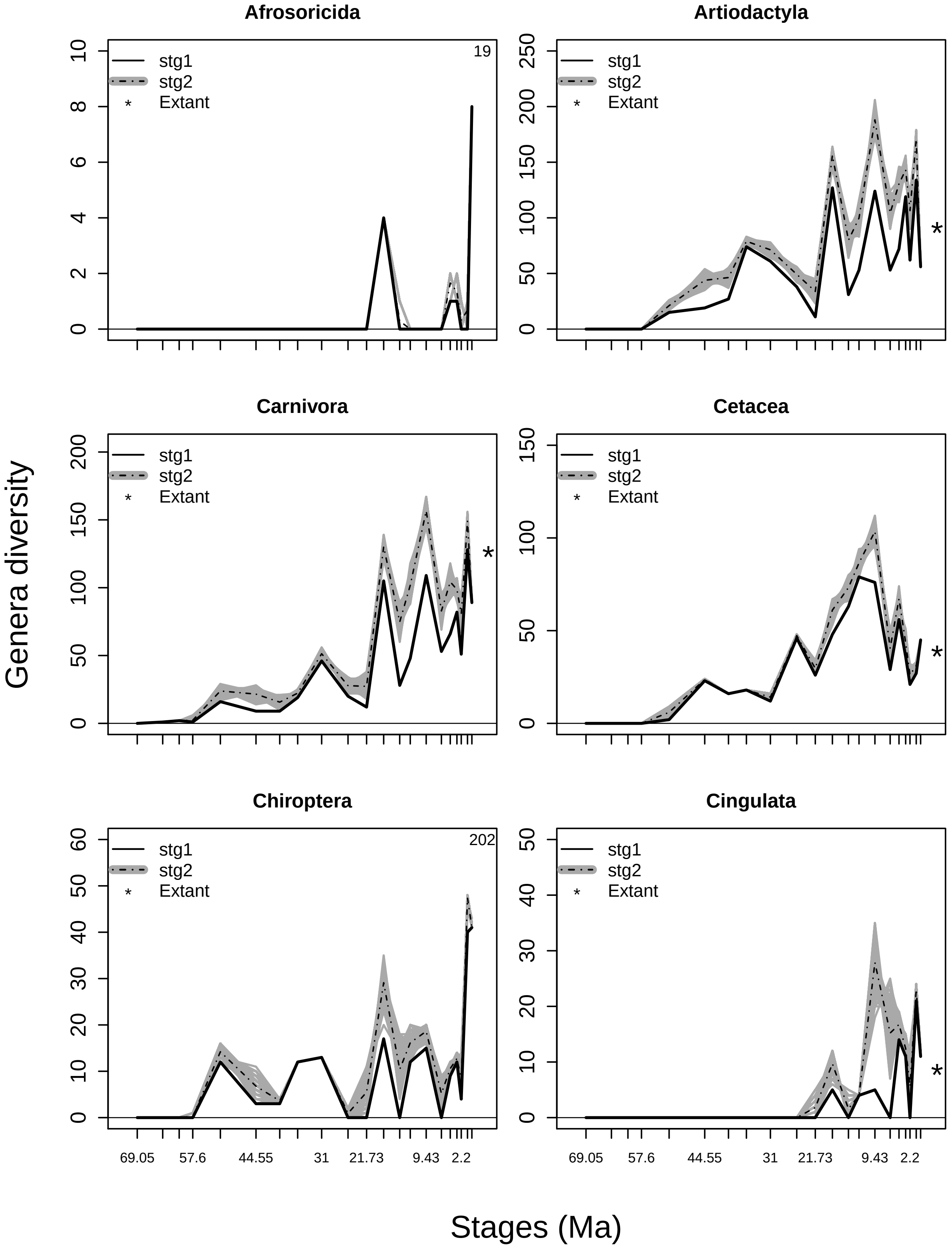
| Order | extinction risk |
|---|---|
| Carnivora | 0.14 |
| Pholidota | 0.33 |
| Perissodactyla | 0.83 |
| Chiroptera | 0.05 |
| Cetacea | 0.12 |
| Artiodactyla | 0.22 |
| Soricomorpha | 0.09 |
| Erinaceomorpha | 0.20 |
| Primates | 0.48 |
| Dermoptera | 0.00 |
| Scandentia | 0.00 |
| Rodentia | 0.12 |
| Lagomorpha | 0.38 |
| Proboscidea | 0.50 |
| Sirenia | 0.33 |
| Hyracoidea | 0.00 |
| Macroscelidea | 0.00 |
| Afrosoricida | 0.20 |
| Tubulidentata | 0.00 |
| Pilosa | 0.00 |
| Cingulata | 0.00 |



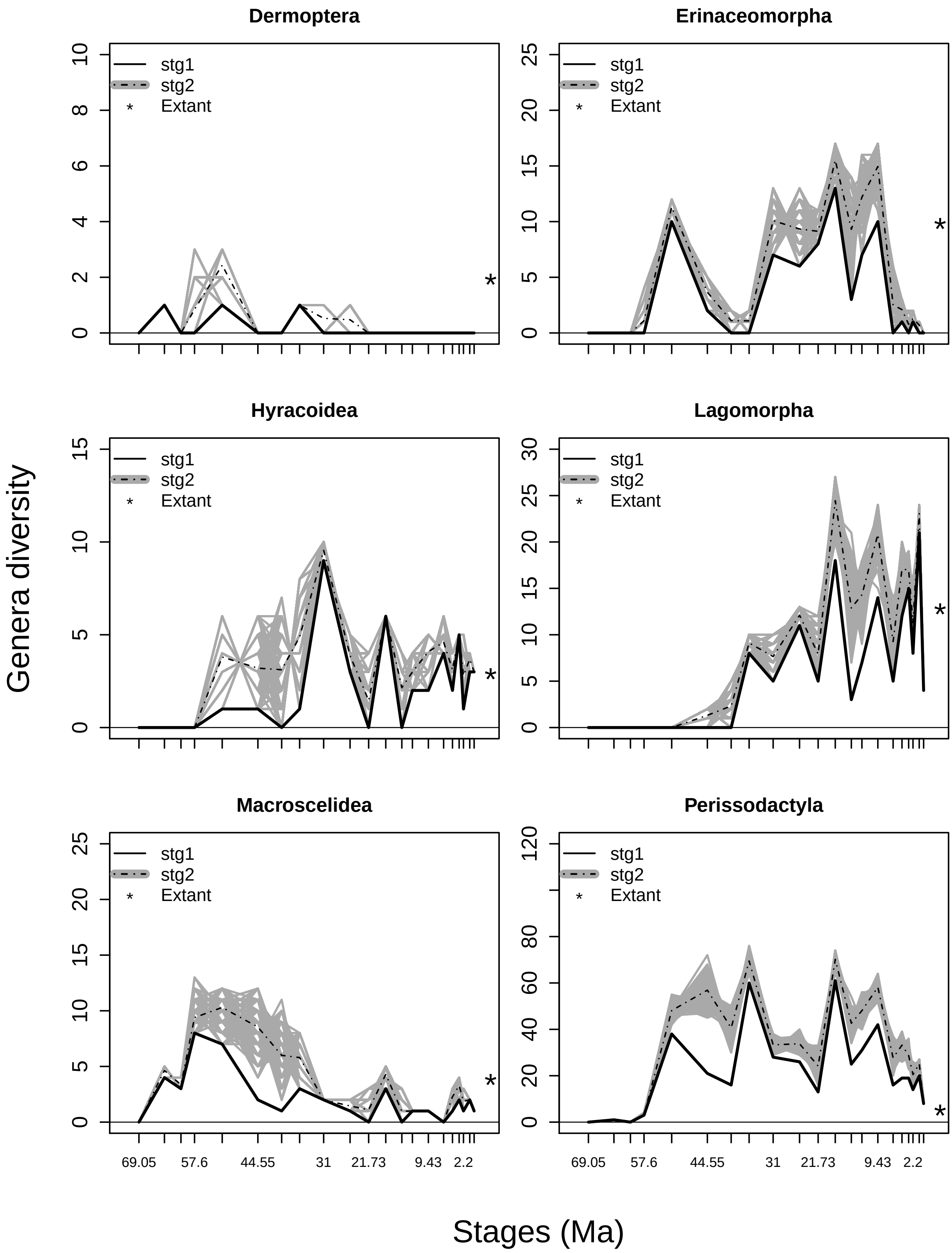
**Appendix VI:** Correlation between the extinction risk and the decline of diversity. Top: boundary-crosser estimate. Middle: gap-analysis estimate. Bottom: perCapita rates of diversification estimate.

**Table IV:** Frequency ratio and body mass estimates for the 21 orders of Placentalia.

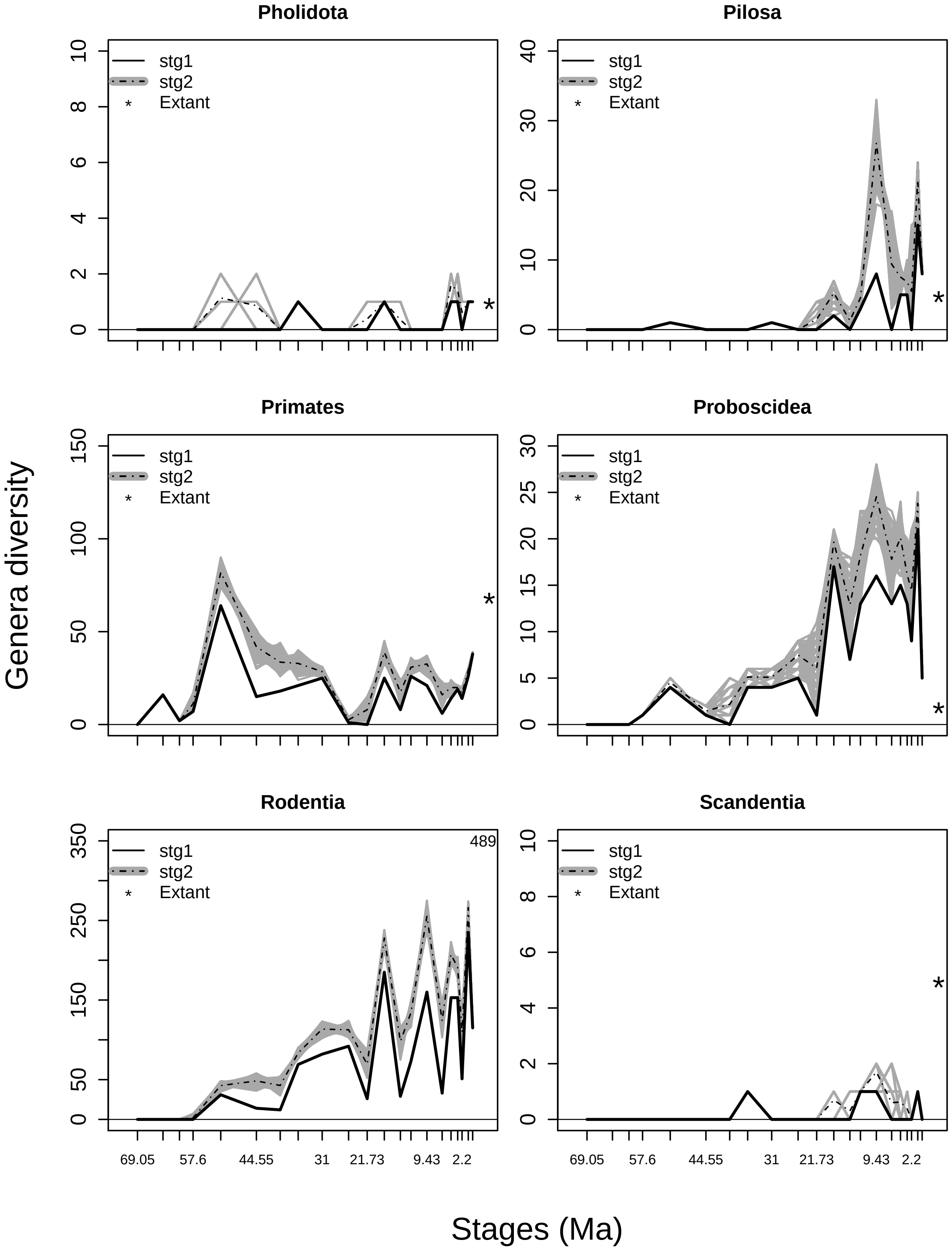
| Order | freqRatio | mass |
|---|---|---|
| Carnivora | 0.57 | 8.13 |
| Pholidota | - | 8.63 |
| Perissodactyla | 0.42 | 12.98 |
| Chiroptera | 0.75 | 2.43 |
| Cetacea | 0.33 | 13.15 |
| Artiodactyla | 0.5 | 10.58 |
| Soricomorpha | 0.3 | 2.14 |
| Erinaceomorpha | 0.32 | 5.48 |
| Primates | 0.17 | 7.12 |
| Dermoptera | - | 7.07 |
| Scandentia | - | 4.82 |
| Rodentia | 0.37 | 4.17 |
| Lagomorpha | 0.11 | 6.41 |
| Proboscidea | 0.08 | 15.15 |
| Sirenia | 0.8 | 12.93 |
| Hyracoidea | 0.07 | 7.98 |
| Macroscelidea | - | 4.24 |
| Afrosoricida | - | 3.19 |
| Tubulidentata | 0 | 10.87 |
| Pilosa | 0.16 | 8.16 |
| Cingulata | 0.84 | 7.31 |



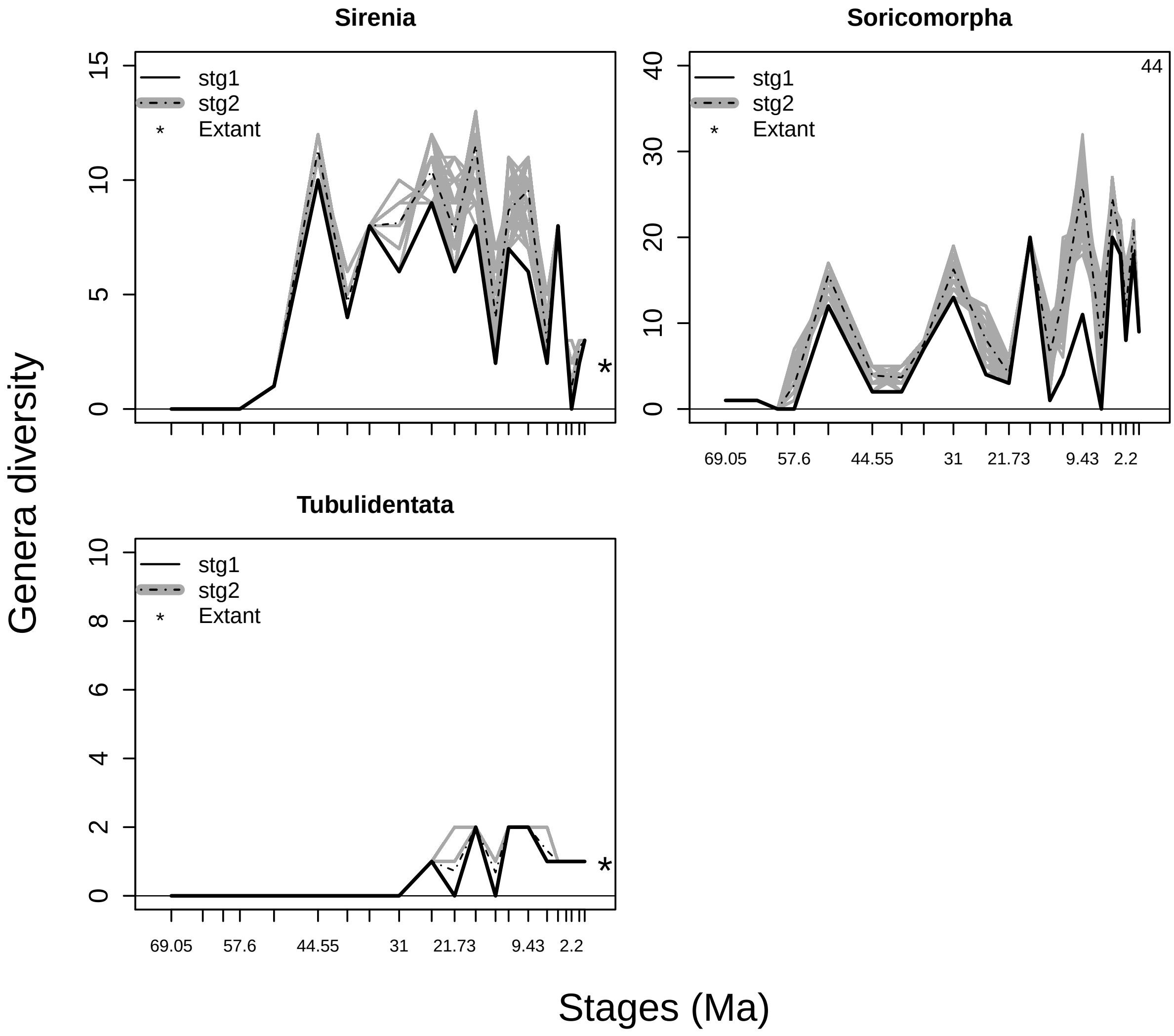
**Appendix VII:** Diversity through time estimated with the sampled in bin method.



Appendix VII cont.



Appendix VII cont.



Appendix VII cont.